DEFENDERS OF WILDLIFE
PRAIRIE DOG COALITION
THE HUMANE SOCIETY OF THE UNITED STATES
WWF

May 20, 2019

Russell Bacon, Forest Supervisor
Monique Nelson, Interdisciplinary Team Leader
Medicine Bow-Routt National Forests and Thunder Basin National Grassland
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Laramie, Wyoming 82070

Dear Mr. Bacon and Ms. Nelson:

Please accept the following scoping comments on behalf of Defenders of Wildlife, Prairie Dog Coalition of the Humane Society of the United States, and World Wildlife Fund on the proposed amendment to the Thunder Basin National Grassland Land and Resource Management Plan (LRMP) of 2001, as amended. The Forest Service initiated a public scoping comment period on April 18, 2019 with a notice of intent (84 Fed. Reg. 16240). We have reviewed the Proposed Action and all supporting materials made available by the Forest Service and have provided what we hope are helpful recommendations and supporting information to be incorporated into the public record.

We submit these comments and associated information in the spirit of continued collaboration with the Forest Service and ask that you please address them carefully as you progress through the amendment planning process. Each of the undersigned organizations has dedicated a substantial amount of time and resources to promote the protection and recovery of the Grassland's wildlife, while respecting the Forest Service's multiple use mandate. Our organizations offer considerable expertise on relevant subjects to the proposed amendment, including black-tailed prairie dog and associated species conservation, black-footed ferret recovery, and national forest and grassland management planning.

Defenders of Wildlife. Defenders is a national non-profit conservation organization founded in 1947 dedicated to the protection of all native animals and plants in their natural communities. This includes the prairie dog ecosystem of North America's Great Plains, a focus of ours for many decades. Defenders is a member of the U.S. Fish and Wildlife Service's Black-footed Ferret Recovery Implementation Team and has been active in black-footed ferret recovery since the species was rediscovered in 1981. Current and former staff have published scientific articles on prairie dogs and black-footed ferrets, coauthored the original black-footed ferret recovery plan, and have been involved in Thunder Basin National Grassland management planning and project implementation since scoping began for the 2001 LRMP. We also have significant expertise on the 2012 Planning Rule. We submit these comments on behalf of our more than 1.8 million members and supporters nationwide, including about 3,000 in Wyoming.

Prairie Dog Coalition of the Humane Society of the United States. The Prairie Dog Coalition is committed keeping prairie dogs on the landscape in key conservation areas. We collaborate with other non-profit organizations, agencies, landowners, concerned citizens, and scientists dedicated to the protection of prairie dogs and advancing stronger management plans for the prairie dog ecosystem. To this end, we have aided in the facilitation of the Forest Service's black-tailed prairie dog management plan for the

Thunder Basin National Grassland since 2008. The PDC promotes and conducts conservation projects, advocates for non-lethal management practices and provides educational and outreach resources that advance prairie dog protection and recovery. On the Grassland, we currently collaborate with landowners, the Thunder Basin Prairie Ecosystem Association, Converse County Weed and Pest, and the Forest Service in a pilot vegetative barrier, an economic study analyzing how much it costs a private landowner to provide prairie dog habitat on a productive ranch, and have provided translocation and sylvatic plague management on the ground for nearly a decade.

<u>World Wildlife Fund</u>. As the world's leading conservation organization, WWF works in 100 countries and is supported by more than one million members in the United States and close to five million globally. WWF's unique way of working combines global reach with a foundation in science, involves action at every level from local to global, and ensures the delivery of innovative solutions that meet the needs of both people and nature. Our Northern Great Plains program was established in 2002 to sustain and enhance biodiversity and restore endangered and flagship species throughout the Northern Great Plains. WWF is a member of the U.S. Fish and Wildlife Service's Black-footed Ferret Recovery Implementation Team and seek to fully recover the black-footed ferret and remove it from the Federal List of Endangered and Threatened Wildlife. Since 2010, we have served in partnership with the Forest Service and associated stakeholders on the Thunder Basin National Grassland to help achieve conservation objectives related to the LRMP. We remain committed to this collaborative effort and to transforming human-wildlife conflict to create sustainable solutions for people and wildlife.

We look forward to continuing to work with you as the Grassland's latest amendment process moves forward. Thank you for considering these comments. If you have questions, please do not hesitate to contact us to discuss them.

Sincerely,

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Scoping Comments on the Proposed Amendment to the Thunder Basin National Grassland Management Plan

Defenders of Wildlife
Prairie Dog Coalition of the Humane Society of the United States
World Wildlife Fund
May 20, 2019

I. Executive Summary

Thunder Basin National Grassland is one of the most important places in North America for the prairie dog ecosystem and the many species that depend on black-tailed prairie dogs and the habitat they create, including the endangered black-footed ferret. Now, U.S. Forest Service leadership is proposing to amend the National Grassland's Management Plan to eliminate critical safeguards and allow poisoning and shooting of prairie dogs across the entire Grassland. This significant management change will undermine wildlife conservation and preclude recovery of the black-footed ferret, among the first species listed under the U.S. Endangered Species Act. Adopting and implementing the proposed amendment will likely violate the National Forest Management Act, the Endangered Species Act, and possibly other laws. We oppose the proposed amendment.

The Forest Service alleges to be seeking a "better balance" between prairie dog conservation and other grassland uses. Thunder Basin's Management Plan has already been amended for this purpose, and the last change resulted from compromises made by all stakeholders, including ranchers, conservation groups, and government entities, agreeing to tradeoffs in its development. The current plan has not been adequately implemented in recent years to address the concerns of ranchers regarding prairie dog expansion into areas near private lands or the concerns of conservationists regarding maintaining and protecting prairie dog colonies. Rather than address the problem of inadequate implementation of the current plan, the Forest Service is appearing to undercut years of compromise meant to address conflicts regarding prairie dog management. The Grassland is federal land that belongs to all Americans, and Forest Service officials are required to serve a strong and abiding public interest in conserving natural landscapes and native wildlife as an important part of its multiple use mandate.

The current Management Plan largely protects prairie dogs from poisoning and shooting in Management Area 3.63, an area specifically designated to maintain at least 18,000 acres of prairie dog colonies to support a viable population of black-footed ferrets and conserve other associated species. The "3.63 area" has been managed by the Forest Service as a future ferret reintroduction site since at least 1985. The area is one of the very few places remaining with the ecological potential to sustain 100 breeding adult ferrets, a requirement for ferret recovery. In fact, the U.S. Fish and Wildlife Service has claimed that Thunder Basin "may well be the best existing site across the species' range in 12 western states, Mexico, and Canada that could significantly contribute to [the ferret's] recovery at the present time."[1]

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[1] United States Department of Interior, U.S. Fish and Wildlife Service. 2017. Letter to Mr. Brian Ferebee (Regional Forester, U.S. Forest Service, Rocky Mountain Region) from Ms. Noreen E. Walsh (Regional Director, U.S. Fish and Wildlife Service, Mountain-Prairie Region). May 30.

The proposed amendment would eliminate the Management Area 3.63 designation, comprising 44,426 acres (less than 10%) of the Grassland. The new proposal would create a Management Area 3.67 to emphasize rangelands with short-statured vegetation that manages prairie dog colonies “toward a target of 10,000 acres” (Scoping Document: 11) to support prairie dog associated species yet enables the Forest Service to lethally control prairie dogs if their total area exceeds 7,500 acres in this same area. Keeping prairie dog colonies small, at low densities, and isolated from each other are elements of the proposed management approach, which is certain to increase management costs considerably and conflict with the needs of imperiled prairie dog associated species.

Scientists consider prairie dogs “keystone species” and “ecosystem engineers,” and the Forest Service’s proposal could harm over 100 native vertebrate species and a host of invertebrates that benefit from prairie dogs and their colonies. Since the late 1800s, black-tailed prairie dogs have lost over 98% of the territory they once occupied across the Great Plains. Poisoning, often subsidized by the federal government, significantly contributed to this decline. In the early 1900s, humans inadvertently introduced sylvatic plague, which is an exotic disease that decimates small mammal populations, including prairie dogs. The combined threats of poisoning and plague, and to some extent shooting, have led to downward population trends and the imperilment of prairie dogs along with associated species such as mountain plovers, burrowing owls, swift foxes, ferruginous hawks, and black-footed ferrets. The loss of prairie dogs has been particularly disastrous for black-footed ferrets, which only live in prairie dog colonies and were likely extirpated from the Grassland by the 1980s.

The Forest Service may amend a national forest or grassland management plan if ecological conditions or other significant changes have occurred. However, the Forest Service’s amendment proposal is inappropriate for existing conditions on the Grassland. The Forest Service has claimed active prairie dog colony area expanded to 48,000 acres on federal lands within and near Management Area 3.63 between 2015 and 2017, and the agency appears to be framing this expansion as the change the amendment is meant to address. During this time, the 3.63 area contained its largest known occupancy of burrowing owls, mountain plovers, ferruginous hawks, and swift foxes. Then, a sylvatic plague epizootic in 2017 reduced prairie dog colonies on federal lands within and near Management Area 3.63 to approximately 600 acres, a level which is far below the National Grassland’s ability to sustain viable populations of many associated species by any measure. This Grassland is in crisis, not from a need to increase the ability to eliminate prairie dogs but from a need to take active measures already outlined in the current plan to simultaneously restore prairie dog occupancy and minimize conflicts with adjacent landowners.

Ironically, during the Forest Service’s scoping comment period for the amendment, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services issued its milestone report on biodiversity and ecosystem services. Roughly one million species are currently at risk of extinction—some possibly within the next 10 years. Now more than ever the Forest Service needs to lead the way in providing critical habitat for prairie dogs and the numerous wildlife species associated with their presence on Wyoming’s Thunder Basin National Grassland. The Forest Service can contribute to the recovery of the black-footed ferret and simultaneously honor its multiple use mandate, including livestock grazing, as they are not mutually exclusive.

In lieu of substantially reducing prairie dog populations and eliminating the Management Area 3.63 emphasis on black-footed ferret reintroduction to address the concerns of neighboring landowners and livestock permittees, the Forest Service should focus on improving collaborative efforts that can transform social conflict and create sustainable solutions for people and wildlife.[2] This could result in lasting outcomes related to prairie dog management on Thunder Basin National Grassland and enable an atmosphere of shared problem-solving that ultimately benefits both the people and wildlife.

II. Introduction

The U.S. Forest Service is proposing to amend prairie dog management direction in its 2001 Land and Resource Management Plan ("Management Plan") for the Thunder Basin National Grassland ("Thunder Basin" or "Grassland") to "place greater emphasis on control and active management of prairie dog colonies to address significant concerns related to health, safety, and economic impacts on neighboring landowners" as stated in the Scoping Cover Letter (p.1). The Forest Service has outlined its proposal in its Notice of Intent ("Scoping Notice") to prepare an Environmental Impact Statement ("EIS") (84 Fed. Reg. 16240), *2020 Thunder Basin National Grassland Plan Amendment, Scoping Document* ("Scoping Document"), and *Proposed Action: Changes to Grassland Plan Direction* ("Proposed Action"), made public on April 18, 2019.

We—Defenders of Wildlife ("Defenders"), Prairie Dog Coalition of the Humane Society of United States ("PDC"), and World Wildlife Fund ("WWF")—oppose the proposed amendment for Thunder Basin, as described by the Scoping Document and illustrated in the Proposed Action. It is likely to violate and fail to support the objectives of several federal laws, including the National Forest Management Act ("NFMA"), 16 U.S.C. §§ 1600 *et seq*.; the National Environmental Policy Act ("NEPA"), 42 U.S.C. §§ 4321 *et seq*.; the Endangered Species Act ("ESA"), 16 U.S.C. §§ 1531 *et seq*; and other laws. Not only is the proposed amendment likely to fail to comply with federal law, it will preclude recovery for the federally endangered black-footed ferret (*Mustela nigripes*; "ferret") and will put other imperiled species at an even greater risk of extinction. Importantly, it also ignores the root cause of the stated concerns by both livestock interests and conservation interests, which is lack of adequate implementation of the current plan's direction for both prairie dog management and conservation.

The proposal's substantial removal of protections to allow for more poisoning and shooting of prairie dogs does not change the issue of lack of past implementation, but it does lead to renewed and increased conflict on an issue that has been addressed previously and significantly in multiple public participation processes. This diversion of resources and time from current plan implementation to yet another plan amendment process will lead to more conflict, not less.

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[2] Madden, F. and B. McQuinn. 2014. Conservation's blind spot: The case for conflict transformation in wildlife conservation. Biological Conservation. 178: 97-106.

We have financially and physically invested in restoring prairie dog populations for the important role they play in grassland conservation, including black-footed ferret recovery. On Buffalo Gap and Thunder Basin National Grasslands our three organizations have collaborated with the Forest Service and other stakeholders to secure, restore, protect, and expand ferret habitat. In addition, Defenders and WWF are longtime Executive Committee members of the U.S. Fish and Wildlife Service's Black-footed Ferret Recovery Implementation Team, the governing body for ferret recovery. Collectively, our organizations have invested millions of dollars to advance recovery of prairie dogs and ferrets on federal, tribal, and private lands in the North American Great Plains. We remain committed to conserving and restoring prairie dog populations on both grasslands because they are two of the few remaining, intact grassland habitats in North America capable of supporting viable black-footed ferret populations.

III. Failure to Implement the Current Management Plan, including the Black-tailed Prairie Dog Conservation Assessment and Strategy

If the Forest Service was adequately implementing the Grassland's Management Plan, including Amendment #3, and the Black-tailed Prairie Dog Conservation Assessment and Strategy ("Strategy") to reduce conflicts related to prairie dog conservation and management, this proposed amendment would not be needed. The Strategy was developed in 2009, and modified in 2015, to "provide overall guidance for prairie dog management on Thunder Basin National Grassland." Livestock grazing is one of the primary uses of the Grassland and surrounding state and private land. The Strategy includes a range of management tools to maintain viable populations of prairie dog and prairie dog associated species while also providing methods for inhibiting unwanted prairie dog colony expansion onto neighboring private lands.

Management options "are bounded by direction contained in the Revised Thunder Basin National Grassland Land and Resource Management Plan (2001 Grassland Plan) and the Record of Decision for the Thunder Basin National Grassland Prairie Dog Management Strategy and Land and Resource Management Plan Amendment #3 (2009)." Amendment #3 added a mandatory plan component to the Land and Resource Management Plan (Chapter 1 - Standard F-65b), which directed the Forest Service to "[a]dopt and implement a black-tailed prairie dog management strategy." Standard F-65b also made the Strategy "a part of" the Plan, giving it the force of law.

Developing Amendment #3 and guidance documents required considerable effort and resources from the Forest Service as well as multiple stakeholders who invested significant time in this process. The resulting strategies reflect compromises made by grazing lessees, nearby landowners, and wildlife conservation organizations. The components, objectives, and tools outlined in the Strategy provided the specific prescriptions for conserving prairie dogs to promote biodiversity and support persistence of prairie dog associated species—all vital for maintaining resistance, resilience, and redundancy in the prairie dog ecosystem of Thunder Basin's mixed-grass prairie, even in the face of plague. The Plan and Strategy ensure protections for wildlife, all the while enabling significant continued use of the Grassland for livestock grazing and allowing for actions to reduce livestock – prairie dog conflicts. Yet, after a promising start, the Forest Service has largely abandoned its commitments made in the Strategy.

The first year of the Strategy's implementation was in 2010. That same year, Defenders, the PDC, and WWF were invited by the Forest Service to lend our expertise to address expanding prairie dog populations within Management Area 3.63: Black-footed Ferret Reintroduction Habitat. Management Area 3.63 serves to provide "adequate amounts and distributions of occupied prairie dog colonies to support the reintroduction of the federally listed endangered black-footed ferret." The tools available in the Strategy to achieve this include prescribed fire, prairie dog translocation, buffer fences with tall vegetation, and sylvatic plague mitigation; the area also has a shooting restriction on prairie dogs. In addition to promoting prairie dog colony expansion in Management Area 3.63, the goal of implementing the Strategy is also to "proactively manage prairie dog populations on the TBNG in an environmentally, biologically, and socially acceptable manner" to prevent undesirable prairie dog colony expansion from the Grassland onto adjoining private lands.

In partnership with the Forest Service, with approval of the Wyoming Game and Fish Commission, and in accordance with the Management Plan and Strategy, we live-trapped prairie dogs from federal land colonies adjacent to private lands on the Management Area 3.63 perimeter and relocated them into the center of Management Area 3.63, applied deltamethrin dust to protect them from plague, and established two fenced buffers to discourage unwanted prairie dog colony expansion. As prairie dog populations began to expand, the Forest Service halted use of these tools, removed the shooting closure, and focused solely on lethal control of prairie dog colonies. Outlined below is the sequence of events that highlight how the Forest Service failed to adequately implement the Strategy, which led to the substantial expansion of prairie dog colonies in 2016/2017 in conflict areas near private lands followed by severe population declines in 2017/2018, including in areas where the plan calls for protections:

1. <u>The Forest Service discontinued the use of prescribed fire to expand prairie dog colonies in Management Area 3.63</u>. This occurred annually during 2009-2012 to promote prairie dog colony expansion and favorable habitat conditions for mountain plovers. It was halted by the Forest Service at the end of 2012 due to ". . .an unstable political climate surrounding prairie dog management Thunder Basin NG" (USFS, TBNG 2014: 3).
2. <u>The Forest Service discontinued the use of translocation</u> in 2012 (a non-lethal tool to mitigate conflicts and encroachment of prairie dogs on adjacent private lands) due to a request by the Wyoming Game and Fish Commission. "As with prescribed fire, due to an unstable political climate surrounding prairie dog management on Thunder Basin NG, translocation has been precluded as an implementation tool since 2011," (USFS, TBNG 2014: 4).
3. In 2012, in response to a complaint by an adjacent landowner, <u>the Forest Service removed one of the two permanent buffer fences</u> (constructed in 2010 to benefit the said landowner) along federal-private land boundaries designed to create a vegetative buffer and prevent future recolonization of the area by prairie dogs. The buffer that remained had been effective

according to Forest Service monitoring reports but the buffer that was removed due to landowner pressure returned to full prairie dog occupancy upon removal of the fence (USFS, TBNG 2014: 7).

4. The Forest Service rescinded the prairie dog shooting closure, beginning March 3, 2017, stating in the agency press release that it was due to "high populations of prairie dogs" and the need to "curb significant prairie dog colony expansion" (USFS, MBRNF & TBNG 2017). The closure was originally established in 2001 for Management Area 3.63. While the ban was apparently reinstated on March 27, 2019, closure signage has not been posted nor has an agency news release been circulated.
5. In 2017, the Forest Service halted the application of deltamethrin (to curtail plague) into prairie dog burrows within Management Area 3.63 even though active plague was occurring Grassland wide.[3]

Deputy Regional Forester Jacqueline Buchanan, during our June 14, 2017 meeting in Denver, acknowledged that the *Black-tailed Prairie Dog Conservation Assessment and Strategy* had not been properly executed.[4] The Forest Service did not adequately implement tools available and permissible in the Strategy to limit prairie dog colony expansion into unwanted areas. Per the examples above, the agency also did not adequately implement tools available to maintain colonies in Management Area 3.63 and other areas where desired. In fact, Forest Service leadership actively opposed implementation of conservation tools available. Offers from our organizations to provide materials and assistance to implement the conservation aspects of the plan in Management Area 3.63 were not accepted, and Regional Forester Brian Ferebee sent a letter to the Wyoming County Commissioners Association on May 19, 2017 assuring the commissioners that the Forest Service would not conduct plague mitigation measures on the Grassland. Soon after, a plague epizootic was first detected in June 2017 and quickly spread across the Grassland, reducing the active colonies on federal lands in and near Management Area 3.63 to approximately 600 acres (Scoping Document: 6).

These Forest Service decisions were not consistent with the Plan. Per the Strategy, "Plague management tools (e.g., dusting and vaccination) will be used where practical and effective to control plague within prairie dog complexes." Just after plague was detected on the Grassland, Defenders, PDC, and WWF made repeated requests in meetings and letters to the Forest Service to immediately apply deltamethrin dust to prairie dog burrows to protect prairie dogs in Management Area 3.63 that we collectively recovered. Application of deltamethrin, which our organizations had purchased and provided to Grassland managers, may have halted the spread of plague outbreak and promoted the conservation of

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[3] Letter from Mr. Brian Ferebee, (Regional Forester of the Rocky Mountain Region) to the Wyoming County Commissioners Association. May 19, 2017; Email from Mr. Dennis Jaeger, Forest Supervisor (Medicine Bow-Routt National Forests, Thunder Basin National Grassland) to Wyoming County Commissioners Association, Subject: Short-term and long-term actions for Thunder Basin National Grassland. May 19, 2017.

[4] Letter from Chamois Andersen (Defenders of Wildlife), Lindsey Sterling-Krank (Prairie Dog Coalition), Kristy Bly (World Wildlife Fund) to Brian Ferebee (U.S. Forest Service, Denver Regional Office), Subject: Follow-up to meeting on Thunder Basin National Grassland. June 30, 2017.

mountain plovers and burrowing owls that had returned with the prairie dog recovery. This plague mitigation tool was denied on multiple occasions[5] by the Forest Service. The 2017/2018 plague event resulted in a near total loss of the prairie dog populations and associated wildlife species in Management Area 3.63 and beyond. In addition, the significant financial federal and non-federal conservation investments to recover prairie dog populations in this area were lost.

For nearly 12 years, our organizations have dedicated significant time, labor, and resources for prairie dog conservation within Management Area 3.63. Collectively, we have invested more than $200,000 toward a host of conservation efforts on Thunder Basin, including the translocation of prairie dogs from boundary areas of conflict near private land into the core conservation area when acreage was below the objective. Our organizations also purchased and donated deltamethrin, which was stored by the Forest Service and the National Black-footed Ferret Conservation Center and on hand if a plague epizootic occurred, but which has remained unused in recent years and, as noted above, prohibited from use by Regional Forester Ferebee's instruction.[6] This and other failures to manage Thunder Basin and Management Area 3.63 in accordance with the Plan and Strategy resulted in squandered resources, increased social conflict, and significant adverse impacts to the Grassland's wildlife and potential to serve as a critical part of ferret recovery.

IV. Status of black-footed ferret recovery

Approximately 350 black-footed ferrets live in the wild today, which is far short of the numbers needed to recover the species.[7] To remove the black-footed ferret from the Federal List of Threatened and Endangered Species, 3,000 breeding adult ferrets need to persist for three years at 30 sites (USFWS 2013). Of those 30 sites, 10 sites need to host at least 100 breeding adults and 20 sites need to host at least 30 breeding adults (USFWS 2013). Of the 29 reintroduction sites established to date, only half support active ferret populations, and most of these sites require continued supplementation of captive-bred animals.[8]

Notably, there are few sites in the ferret's range with sufficiently large prairie dog complexes to support 100 adult ferrets. In 2007, at the peak of ferret populations in the wild, there were only five reintroduction sites that hosted, or had the near potential to host, 100 breeding adults[9]. Today, there

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[5] Letter from Mr. Brian Ferebee, (Regional Forester of the Rocky Mountain Region) to the Wyoming County Commissioners Association. May 19, 2017.

[6] Letter from Mr. Brian Ferebee, (Regional Forester of the Rocky Mountain Region) to the Wyoming County Commissioners Association. May 19, 2017.

[7] BFFRIT (Black-footed Ferret Recovery Implementation Team) Conservation Subcommittee. 2019. BFF [black-footed ferret] Site Estimates 2018, Table. Presented at April 10, 2019 meeting, Fort Collins, Colorado.

[8] BFFRIT (Black-footed Ferret Recovery Implementation Team) Conservation Subcommittee, 2019. BFF [black-footed ferret] Site Estimates 2018, Table. Presented at April 10, 2019 meeting, Fort Collins, Colorado.

[9] BFFRIT (Black-footed Ferret Recovery Implementation Team) Conservation Subcommittee, 2019. BFF [black-footed ferret] Site Estimates 2018, Table. Presented at April 10, 2019 meeting, Fort Collins, Colorado.

are no reintroduction sites with 100 breeding adults due to sylvatic plague, drought, and other factors. Although efforts are underway to increase ferret numbers at those sites, at least five additional sites capable of hosting 100 breeding adult ferrets are needed to achieve delisting objectives.[10] With the right management approach, Thunder Basin has the potential to support 100 breeding adults; adoption of the Forest Service's proposed amendment, however, will preclude black-footed ferret recovery.

V. Need to Amend the Management Plan

A. NFMA and NEPA regulations require the Forest Service to adequately describe and justify a legitimate purpose and need to amend the Thunder Basin Plan.

Defining a "need to change" a national forest or grassland management plan under NFMA and its associated planning regulations ("2012 Planning Rule") (36 C.F.R. § 219) and a "purpose and need" for an action under NEPA and its associated regulations (40 C.F.R. § 1500) are closely related processes. After identifying a legitimate basis for changing a plan under the 2012 Planning Rule, the Responsible Official should then incorporate the need to change as an aspect of the purpose and need in NEPA documents associated with an amendment (FSH 1909.12, ch. 20, § 21.13(2); FSH 1909.12, ch. 20, § 21.21(4); FSH 1909.12, ch. 20, § 21.3(1)–(4)). This helps ensure consistency and compliance with both laws. Moreover, the requirement that there be a justifiable basis for amending a plan helps to ensure that the Forest Service wisely stewards the public's resources.

The Forest Service must provide justification for amending the Grassland Management Plan that meets the criteria established by NFMA. Although NFMA authorizes the Forest Service to amend forest plans, this authorization is accompanied by crucial limitations to prevent arbitrary amendments. Pursuant to the 2012 Planning Rule, an amendment must be based on a "preliminary identification of the need to change the plan," which may be based on "a new assessment; a monitoring report; or other documentation of *new* information, changed conditions, or changed circumstances" (36 C.F.R. § 219.13(b)(1) (emphasis added)). As the Forest Service recognizes, amendments are intended to keep plans "*current*, *effective*, and relevant" (FSH 1909.12, ch. 20, § 21.3). Forest Service Directives further caution that "[a] well-supported and effective rationale determining a need to change the plan *must be based on a good source of information*" (FSH 1909.12, ch. 20, § 21.2). In light of these limitations, an amendment that relies on irrelevant factors (such as outdated information or no-longer-extant conditions) would be arbitrary.

In sum, satisfying the letter and the spirit of NFMA and the Planning Rule requires the Responsible Official to present the new information and, importantly, to explain why the new information renders the existing forest plan language inadequate. This is not a political, but a science-based, inquiry. The Planning Rule states that "[t]he responsible official shall document how the best available scientific information ("BASI") was used to inform the amendment decision…" (36 C.F.R. § 219.3). Moreover,

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[10] BFFRIT (Black-footed Ferret Recovery Implementation Team) Conservation Subcommittee, 2019. BFF [black-footed ferret] Site Estimates 2018, Table. Presented at April 10, 2019 meeting, Fort Collins, Colorado.

"[s]uch documentation must: Identify what information was determined to be the best available scientific information, explain the basis for that determination, and explain how the information was applied to the issues considered" (36 C.F.R. § 219.3). The planning Directives provide further support for and guidance to uphold these requirements (FSH 1909.12, ch. 20, § 21.2; FSH 1909.12, ch. 20, § 21.21).

With respect to NEPA regulations, a purpose and need statement should be brief but also specific (40 C.F.R. § 1502.13). However, the purpose and need for the amendment must be reasonable in light of the information the Forest Service has before it. The purpose and need cannot be defined as to make the Forest Service's preferred result "a foreordained formality." *Citizens Against Burlington, Inc. v. Busey*, 938 F.2d 190, 196 (D.C. Cir. 1991). Instead, "an agency should always consider the views of Congress, expressed, to the extent that the agency can determine them, in the agency's statutory authorization to act, as well as in other congressional directives." *Id*. Congress's views, of course, are reflected in statutes such as NFMA—and the ESA, which has made conservation and recovery of listed species an integral part of the Forest Service's mission. In light of the Forest Service's obligations under NFMA and NEPA to describe a legitimate, justified, and non-arbitrary basis for amending a plan, we discuss specifics of the Scoping Document below.

B. The Forest Service fails to demonstrate the need for a plan amendment.

1. The Scoping Document provided no direct evidence that "a new assessment; a monitoring report; or other documentation of new information, changed conditions, or changed circumstances" have emerged on the TBNG since Amendment #3 was implemented in 2009 (as required by 36 C.F.R. § 219.13(b)(1)).

The Scoping Document does not identify and document what new information provides the basis for changing the Management Plan in accordance with 36 C.F.R. § 219.13(b)(1). We recognize that the Draft Environmental Impact Statement (DEIS) will provide a more detailed analysis of conditions on Thunder Basin that purportedly justify changing the Management Plan. Yet the 2012 Planning Rule requires the "*preliminary identification* of the need to change be based on…*documentation* of new information, changed conditions, or changed circumstances" (36 C.F.R. § 219.13(b)(1)). Given the specificity presented in the need statements and Proposed Action, the Scoping Document should make stronger connections between the need statements and the supporting documentation required by the Planning Rule. Instead of specifically identifying and justifying a need for change, however, the Scoping Document makes non-specific inferences that only loosely connect with stated needs.

For example, the Scoping Document alludes to a "collaborative stakeholder group" convened by the State of Wyoming, which "provided a recommendation that has served as the basis for this proposed action" (Scoping Document: 5). To enable transparency, documentation of this collaborative process and rationale for the recommendation must be provided, and the Forest Service must include a list of non-governmental organizations (NGOs) that were included in this process and identify those that agreed to the recommendation. To be clear, this collaborative stakeholder group recommendation was *not* consensus-based and does *not* reflect the views or recommendations of the Conservation Organizations who have signed this letter.

As another example, the Scoping Document implies that the expansion of prairie dog colonies beginning in 2015 constitutes a significant change in Grassland conditions:

> Not long after the Forest Service completed an update to the management strategy in 2015, active prairie dog colonies on and around the Thunder Basin began to expand significantly. The population expansion continued into 2016 and 2017, exceeding anything seen in recent history (figure 2 and figure 3). Mapping efforts during these years showed that active prairie dog colonies expanded to over 75,000 acres, more than doubling the previous record for mapped acres. (Scoping Document: 5)

Prairie dog expansion in 2015-2017 does not constitute a significant change in Grassland conditions. The 75,000-acre number cited in the Scoping Document is for all landownerships in this general area, including private lands; 48,000 acres is the amount on federal land (Scoping Document: 6). The Biological Assessment and Evaluation for the 2001 Northern Great Plains Management Plans Revision (USFS 2001) accurately predicted and expected prairie dog colony expansion up to 48,000 acres on federal land even earlier, by 2011-12 “if drought conditions prevail and vegetation conditions are conducive” (p. 102).

Annual monitoring reports required by the Management Plan would be very useful in evaluating this issue, particularly because black-tailed prairie dogs are management indicator species. However, the Forest Service has not compiled any plan monitoring reports beyond 2011 (M. Nelson email May 13, 2019). Moreover, the Scoping Document is internally inconsistent with respect to prairie dog expansion justifying the need to change. The Scoping Document later notes that, “[i]n 2017, a plague event reduced the number of mapped acres by 99 percent to the current level of approximately 1,000 acres of active prairie dog colonies.” In other words, some information that the Forest Service is relying on was already out-of-date and invalid before the proposal to amend the plan was announced. One-thousand acres of prairie dogs – of which approximately 600 acres is on the Grassland in the vicinity of Management Area 3.63 – is well below any accepted scientific standard for enabling a viable ferret population and possibly for conserving well-distributed populations of prairie dogs and associated species across the grassland ecosystem.

In short, the Scoping Document fails to document new information, changed conditions, or changed circumstances that justify amending the Plan. Moreover, the information that is available (*e.g.*, the recent loss of significant active prairie dog acres to plague) does not support the proposed changes to the plan. Accordingly, the proposed amendment, as described by the Scoping Document and Proposed Action, is arbitrary.

2. The Forest Service’s stated purpose for the amendment is vague and arbitrary.

The Forest Service's stated purpose certainly adheres to the NEPA regulations' direction that it be "brief"—but it is otherwise deficient. The proposal to "to amend the grassland plan to better balance prairie dog colony conservation and control with other grassland uses" fails to "specify the underlying purpose" (40 C.F.R. § 1502.13) because it does not specifically define what "better balance" means. The Forest Service provides no explanation or evidence regarding how the grassland plan has resulted in a lack of "balance" among grassland uses. It provides no explanation or evidence how removing protections for a species that is a keystone for the grassland ecosystem (and critical for black-footed ferret recovery, in particular) is "better" for Thunder Basin. Without these explanations and this evidence, the proposed amendment appears to simply be political acquiescence. As discussed below, this perception is only bolstered by the stated list of needs, which appear to have been "reverse engineered" to fit the proposed action. Creating "needs" that point to a predetermined outcome can violate NEPA by, among other things, resulting in the improper elimination of the no-action alternative or alternatives that better support wildlife and listed species recovery.

3. The needs outlined in the Scoping Document, listed and addressed below, fail to demonstrate a necessity to amend the management plan.

The Scoping Document lists seven needs for the proposed amendment. None are accompanied by a science-based rationale or other adequate justification in the Scoping Document. We look at these in turn.

a) "Refocus management in management area 3.63, "black-footed ferret reintroduction habitat," to emphasize rangelands with short-stature vegetation that provide for multiple uses, including providing habitat for prairie dogs and associated species and providing livestock forage." (Scoping Document: 7)

This stated need is misleading. The proposal is not merely intended to ***refocus*** management area 3.63 management, but to ***eliminate*** the 3.63 management area designation from the Grassland entirely and stymie ferret recovery on the Grassland for the foreseeable future.

Simply "providing habitat" fails to meet requirements under 36 C.F.R. § 219.8 and 36 C.F.R. § 219.9 of the 2012 Planning Rule. Any amendment must ensure that the management plan maintains and restores the ecological integrity of the shortgrass prairie ecosystem, which many scientists call "the prairie dog ecosystem," because prairie dogs are essential to this system (Miller et al. 1994; Mulhern and Knowles 1996; Kotliar et al. 1999; Bangert and Slobodchikoff 2006; Hanson et al. 2007; Santos-Barrera et al. 2008). An amendment must take into account, for example, "[c]onditions in the broader landscape that may influence the sustainability of resources and ecosystems within the plan area" (36 C.F.R. § 219.8(a)(1)(iii)); thus, the amendment process and outcome must thoroughly address how livestock grazing affects grassland ecosystem conditions, including prairie dogs and associated species—not just how prairie dogs may be affecting livestock production (see Knopf 1996; Fuhlendorf et al. 2010; Kohl et al. 2013).

Further, the EIS for the amendment must take into account the level of prairie dog poisoning occurring in the "broader landscape," beyond the Grassland boundaries. The process and amendment must take into account "[s]ystem drivers, including dominant ecological processes, disturbance regimes, and stressors, such as natural succession, wildland fire, invasive species, and climate change," required by 36 C.F.R. § 219.8(a)(1)(iv); and the key driver of the shortgrass prairie ecosystem is the interactive disturbance regime of prairie dogs, bison, fire, and drought (Coppock and Detling 1986; Uresk et al. 1996; Truett et al. 2001), with periodic occurrences of extreme drought conditions like that which occurred in 2017 (Wang et al. 2019). Extensive poisoning removes prairie dogs from the equation and likely has significant effects that upset these natural processes.

b) "Delineate more logical boundaries for management area 3.63, for example by strategically using natural topographic and hydrologic barriers and incorporating boundary management zones." (Scoping Document: 7)

The Forest Service is proposing to have zero acres of management area 3.63 designated in the Grassland. Delineating management area boundaries based on natural barriers may make sense for reducing federal to private boundary conflicts, but the Forest Service must provide a rationale to support why this is a need. The purported need to change the boundaries of Management Area 3.63 is fundamentally undermined by the fact that the Forest Service intends to eliminate prairie dog protections within the area, as discussed next.

c) "Increase the availability of management options for prairie dog colony conservation and control, including lethal prairie dog control within management area 3.63." (Scoping Document: 7)

Discussion in the Scoping Document is limited to increasing the availability of management options for control; no examples of increased options for conservation are mentioned. Allowing an increase in lethal control in the 3.63 management area beyond the exceptions already allowed for private land and residence buffers undermines the management area designation's purpose: ferret recovery. Moreover, the Forest Service's Proposed Action indicates that the amendment will reduce the 3.63 area to zero acres and replace it with a new smaller 3.67 management area designation that will emphasize short stature vegetation but will deemphasize ferret recovery. Based on figures in the Proposed Action, roughly 8% (44,426 acres) of the Grassland is currently designated as management area 3.63, and prairie dog poisoning and shooting are largely allowed on the rest of the Grassland. At last count, as reported in the Scoping Document, the number of active prairie dog colonies on the Grassland in the vicinity of Management Area 3.63 had plummeted to approximately 600 acres; that's about 0.1% of the Grassland. Even at their presumed "record" level of 48,000 acres in the vicinity of Management Area 3.63 (Scoping Document: 6), prairie dog colonies accounted for less than 9% of the Grassland. This is right in line with the predicted range of variation in the 2001 LRMP (Biological Assessment and Evaluation, Appendix H: 102). The Forest Service must explain why it believes the current suite of management options is insufficient to conserve and control prairie dogs.

> d) "More effectively manage prairie dog colony encroachment from the Thunder Basin National Grassland onto private and state land. Encroachment concerns include public health, agricultural production, land values, facilities, and serving as a good neighbor as described in the record of decision for the grassland plan." (Scoping Document: 7)

The current management plan already provides the tools to address encroachment concerns. The Forest Service has not used them in recent years. (See Section III above for details and supporting information.) Increasing the areas where poisoning is allowable will not affect the encroachment issue.

> e) "Ensure management direction identifies habitat requirements needed to support viable populations of prairie dogs and associated species, such as mountain plover, burrowing owl, and swift fox, and that management would not preclude future reintroduction of black-footed ferret." (Scoping Document: 7)

The management plan must contribute to ferret recovery under the ESA and NFMA (see Sections VI and VIII below.) This must be included as a need for the plan amendment. Lowering the bar to "not preclude future reintroduction of black-footed ferret" is not adequate.

This statement also indicates there is a need to know the habitat requirements for supporting viable populations of these species. The Forest Service should conduct an amendment assessment (FSH 1909.12, Ch. 10, § 15) to ascertain whether current management direction does or does not support providing the habitat requirements for maintaining viable populations of the species listed in the need statement above and does or does not provide the ecological conditions to support a black-footed ferret population. The EIS must determine how the amendment changes projected future habitat conditions for these species.

Substantial analysis on the needs of associated species was completed as part of the 2001 LRMP EIS process and led to the current plan direction to manage for a minimum of 18,000 acres of prairie dog colonies in Management Area 3.63. The Proposed Action implies that this analysis was inaccurate and that far fewer, smaller, more scattered, and less protected acres of prairie dog colonies are adequate but provides no scientific basis for this stance.

> f) "Align with the Wyoming Game and Fish Department's "Wyoming Black-footed Ferret Management Plan" (2018)." (Scoping Document, p. 7)

The Forest Service is under no obligation to align any part of its management plan with Wyoming's Black-footed Ferret Management Plan or any state government wildlife management direction (36 C.F.R. § 219.4(b)(3)). Given that there is no statutory or regulatory basis for wholly subjecting federal management of federal public lands to the priorities of a state game agency, Wyoming's plan fails to provide a basis justifying the need to change Thunder Basin's existing management plan, including the 2009 Amendment #3 of Thunder Basin's land management plan. Despite the 2012 Planning Rule's instruction to coordinate with other government entities under 36 C.F.R. § 219.4(b)(1), the Forest Service cannot abdicate its statutory responsibilities to manage the federal public lands in line with Congress's direction.

Notwithstanding any state-federal cooperative agreements or memoranda of understanding, federal agencies have final responsibility for ensuring compliance with federal law. The ESA and NFMA require the Fish and Wildlife Service and the Forest Service to use their authorities to recover listed species and any purported veto power by the State of Wyoming (whether express or implied) is unlawful.

It is a common misconception that states represented by their wildlife agencies have ultimate management authority over wildlife. In fact, the courts have consistently upheld that the federal government has supremacy over its lands under the Property Clause of the United States Constitution (United States Constitution, Article IV, Section 3), which grants Congress the "Power to dispose of and make all needful Rules and Regulations respecting the Territory or other Property belonging to the United States." In *Kleppe v. New Mexico*, 426 U.S. 529, 541 (1976), the Court stated, "the 'complete power' that Congress has over public lands necessarily includes the power to regulate and protect the wildlife living there." *Kleppe* further described the limit of a state's ability to dictate policy on federal lands: "those powers exist only in so far as [their] exercise may be not incompatible with, or restrained by, the rights conveyed to the Federal government by the Constitution." *Id.* at 545 (internal quotes omitted). The Forest Service clearly has the authority to manage wildlife habitat and species populations (Schultz 2012). This includes managing the public's use of wildlife on national forests and grasslands.

Even if aligning with Wyoming's ferret plan was a legitimate action, the Forest Service's Proposed Action will move further away from making progress toward the Wyoming plan's objectives (WGFD and WBFFWG 2018: 11). Although the Forest Service states that ferret reintroduction would not be precluded, the prairie dog acreages and management actions in the proposal are insufficient to support 30 breeding adult ferrets, the minimum required to contribute toward recovery (USFWS 2013). Objective 1 calls for maintaining "a minimum of 341 breeding adults distributed among 5 or more populations statewide," and Wyoming currently contains only two ferret populations. Objective 2: "[m]aintain a minimum of 30 breeding adults in each population, with at least 2 populations containing a minimum of 100 breeding adults," is far from being achieved as only 1 site exists with this potential. Objective 3 aims to "[e]stablish at least 2 populations within white-tailed prairie dog colonies and at least 1 population within black-tailed prairie dog (*C. ludovicianus*) colonies," yet no ferret populations are known to occur on black-tailed prairie dog colonies in Wyoming and no potential black-tailed prairie dog recovery sites have been identified in the State.

Finally, the Forest Service fails to demonstrate how the current Thunder Basin Management Plan is out of alignment with the Wyoming Black-footed Ferret Management Plan. If the lack of alignment is a problem that is preventing the Forest Service from recovering ferrets on the Grassland, the agency must provide documentation that supports its preliminary identification of the need to change the plan. The current emphasis of ferret recovery in the 3.63 area aligns with the U.S. Fish and Wildlife's Black-footed Ferret Recovery Plan and even provides the opportunity for the Grassland to host a minimum of 100 breeding adults, which would greatly advance recovery of the species. If the Forest Service was actively working toward achieving the Wyoming plan's objectives, which would need to fall under federal authority and the ferret recovery plan, the agency would be better off fulfilling the requirements of its current plan so that ferrets could successfully be reintroduced at the 100-breeding adult level.

g) "Enhance engagement with partners for collaborative implementation of new plan direction." (Scoping Document, p. 7)

The meaning and implications of "collaborative implementation" must be clarified. A collaborative group should not be imposing management actions inconsistent with the Forest Service's statutory, regulatory, and plan obligations.

VI. Compliance with the National Forest Management Act

A. The Forest Service must meet NFMA's diversity requirement.

NFMA was enacted in 1976 in large part to elevate the value of ecosystems, habitat, and wildlife on our national forests to the same level as timber harvest and other uses. Specifically, NFMA requires the Forest Service to develop planning regulations that shall "provide for diversity of plant and animal communities based on the suitability and capability of the specific land area in order to meet overall multiple-use objectives" (16 U.S.C. § 1604(g)(3)(B)). In April 2012, the Forest Service finalized regulations implementing the NFMA (See 16 U.S.C. § 1604, 36 C.F.R. § 219). These regulations, the 2012 Planning Rule, established a process for developing and updating forest plans and set conservation requirements that the plans must meet to sustain and restore the diversity of ecosystems, plant and animal communities, and at-risk species.

Crucially, traditional Grassland uses under the multiple-use mandate do not trump NFMA's diversity requirement. Forest Service regulations call for "'integrated resource management,' directing the Forest Service to develop plans that provide for multiple uses '*while*' meeting the needs [of] sustainability and diversity. 36 C.F.R. § 219.10." *Fed. Forest Res. Coal. v. Vilsack*, 100 F.Supp.3d 21, 41 (D.D.C. 2015) (emphasis in original). "This means that the 2012 Planning Rule cannot be faulted for necessarily and inevitably requiring a reduction in [activities such as] timber harvest and grazing due to its sustainability mandates." *Id.* Closely related are NFMA's and the Planning Rule's substantive obligations on the agency to protect and recover species; these likewise cannot be ignored in pursuit of other expectations.

B. The Forest Service must comply with all applicable requirements of the 2012 Planning Rule.

1. Amending a plan (36 C.F.R. § 219.13)

a) The amendment process must be supported by a sufficient basis upon which to change the plan (36 C.F.R. § 219.13(b)(1)).

As demonstrated in Section V of these comments above, there is no information in the Scoping Document that provides a reasonable basis or justification for the Forest Service to expend its limited resources on gutting plan components that protect wildlife—and which are intended to help the agency comply with NFMA and other laws (such as the ESA).

b) The amendment process must provide opportunities for public participation (36 C.F.R. § 219.13(b)(2)).

We appreciate the Forest Service's efforts to engage us and willingness to communicate with us in the proposed amendment planning process. However, we are concerned about the transparency of the public process.

For example, despite our reasonable request, the Forest Service stated it would not make public the names and qualifications of the Interdisciplinary Team ("IDT") members at this time. It is the responsibility of the IDT to prepare plan amendments (36 C.F.R. § 219.5). Among other important guidance that the IDT be directly involved in the public participation process, the Planning Handbook states, "[t]he intensive public participation associated with collaboration is expected to support the following outcomes:"

> 3. Improved capacity of the Interdisciplinary Team and the public to reduce uncertainty by gathering, verifying, and integrating information from a variety of sources;
> …
> 5. Positive public perceptions of plans and the planning process; and
> 6. Increased trust and commitment to the final plan, with reduced potential for litigation.

(FSH 1909.12, ch. 40, § 43.1). Given the lack of transparency to this point, these outcomes appear uncertain for this proposed amendment.

Another example of the lack of transparency is the Forest Service's refusal to disclose the scientific information supporting the purported need to change the Plan before the release of the DEIS. Requirement 36 C.F.R. § 219.4 of the Planning Rule states,

> When developing opportunities for public participation, the responsible official shall take into account the discrete and diverse roles, jurisdictions, responsibilities, and skills of interested and affected parties; the accessibility of the process, opportunities, and information; and the cost, time, and available staffing. The responsible official should be proactive and use contemporary tools, such as the Internet, to engage the public, and should share information in an open way with interested parties.

The Conservation Organizations who have signed this letter offer a significant level of expertise and years of experience in this issue arena. In addition, there are many Black-footed Ferret Recovery Implementation Team Executive Committee members and other ferret, prairie dog, and prairie dog associated species researchers that could also provide relevant science and input to this process. The Forest Service's reticence in providing the information justifying its proposed action thwarts the ability of these many experts to do so—and further undermines the public's perception of and trust in the Forest Service's work.

c) The amendment process must comply with NEPA (36 C.F.R. § 219.13(b)(3)).

In Section VII below, we exhibit how, based on the content of its Scoping Document and Proposed Action, the Forest Service is failing to fully comply with NEPA.

d) New plan components must follow the applicable format for plan components as required by 36 C.F.R. § 219.7 of the planning rule (36 C.F.R. § 219.13(b)(4)).

As discussed in Section V above, the Forest Service has not justified the need for changing or adding plan components, and the undersigned Conservation Organizations disagree that new plan components are necessary. Should the Forest Service proceed, however, any plan direction added or modified by a plan amendment must stringently adhere to the Planning Rule. The Planning Rule provides a description and requirements of each type of plan component (36 C.F.R. § 219.7(e)(1)). The Planning Handbook provides additional guidance.

e) The Scoping Document referenced the substantive requirements directly related to the proposed amendment (36 C.F.R. § 219.13(b)(5)).

The Forest Service stated that the "[s]ubstantive requirements of the 2012 Planning Rule that are likely to be applicable to the amendment are in the Code of Federal Regulations (CFR) at 36 CFR § 219.8(a) "ecological sustainability" and (b) "social and economic sustainability;" 36 CFR § 219.9 "diversity of plant and animal communities;" and 36 CFR § 219.10(a) "integrated resource management for ecosystem services and multiple use" (Scoping Document: 1). While we agree these are the substantive requirements likely to be directly related to the proposed amendment, we reiterate that the proposed amendment process is unjustified and illegal.

f) The Forest Service must identify potential species of conservation concern (SCC) and plan for and manage these species "as if they were" SCC (36 C.F.R. § 219.13(b)(6)).

The Forest Service has indicated that it will identify potential species of conservation concern (SCC) during the proposed amendment development process. The proposed amendment substantially lessens protections for black-tailed prairie dogs, and will accordingly have substantial adverse impacts to the numerous associated species that rely on and benefit from prairie dogs—and possibly to other species, as well. The Planning Rule thus requires that "the responsible official must determine whether [any of those] species is a potential SCC, and if so, apply section § 219.9(b) with respect to that species as if it were an SCC" (36 C.F.R. § 219.13(b)(6)). Specifically, the Forest Service must:

1. Use the best available scientific information to determine whether the proposed amendment's effects will cause substantial concern about the species capability to persist over the long-term [in the plan area/on Thunder Basin/within Management Area 3.63] (36 C.F.R. § 219.9(c); § 219.13(b)(6));
2. Ensure that the modified/added plan components—including any necessary species-specific plan components—provide the ecological conditions necessary to main a viable population of each species (36 C.F.R. § 219.9(b)); and
3. Develop monitoring questions and indicators for ecological conditions required to maintain viable populations of each species (36 C.F.R. §§ 219.12(a)(5)(iii) & (iv); § 219.5(a)(3)).

If the Forest Service decides to continue developing the amendment after scoping, we urge the agency to develop and make public a draft potential SCC list early in the process—well before issuing its notice on the DEIS. The public should be given ample time to provide input on the species identified as SCC, the best available science used, and the process for making these selections. Indeed, the Forest Service's failure to release a list of the species it is considering identifying as potential species of conservation concern is *already* frustrating the public information and participation goals integral to both NFMA and NEPA. In a June 6, 2016, letter to regional foresters, (then) Deputy Chief Weldon stated that the *final* SCC decision should be made "well before the release of the draft environmental impact statement" "to allow the Forest Service to engage with the public about their concerns regarding the SCC before release of the DEIS."[11] The bottom line is this: the primary role of the NEPA process in relation to species of conservation concern is not to *identify potential SCCs but to address effects of the plan amendment on SCCs*, thus providing a basis for determining compliance with the NFMA viability requirement.

(1) Determinations of occurrence in the Plan Area

A species, which is not federally protected under the ESA, for which there is a substantial concern about persistence must be identified as a potential SCC if it is "known to occur in the plan area" (36 C.F.R. §

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[11] Weldon, L.A.C. Deputy Chief, United States Forest Service. Clarification of implementation of the 2012 Planning Rule, Directives, and Regional Foresters Sensitive Species. June 6, 2016.

219.9(c)). In other management planning processes, the Forest Service has erred in rejecting species for SCC identification due to misinterpreting the identification criteria (FSH 1909.12, ch. 10, 12.52).

This is an example of a recurrent issue. According to the Planning Handbook, actual occurrence records may only be discounted if individual occurrences are “accidental” or “transient,” or are “well outside the species’ existing range” (which would presumably make them accidental or transient) (FSH 1909.12, ch. 10, 12.52(c)(1)). The Forest Service must identify migratory species as potential SCC when their seasonal range includes the Grassland. Seasonal habitat on forests for migratory species on forests or grasslands may be essential for maintaining species viability. This may also be true of habitat for some “transient” species in some areas and excluding such species in accordance with the Planning Handbook may violate the requirement of the Planning Rule to contribute to maintaining a viable population of the species within its range. Thus, the Forest Service must identify migratory bird species, such as the burrowing owl, as SCC.

(2) Determinations of substantial concern about long-term persistence

The Responsible Official must identify a species as a potential SCC if “the best available scientific information indicates substantial concern about the species' capability to persist over the long-term in the plan area” (36 C.F.R. § 219.9). “Concern” may be an inapt word choice in this case. The Planning Rule does not direct the Responsible Official to subjectively determine their own level of concern. The question to be addressed is whether the available scientific information indicates that a substantial risk to long-term persistence in the plan area exists. SCC and potential SCC determinations cannot be arbitrary; they must be informed by expert judgements about persistence. This is indicated by the various classifications specified in the Directives.

According to the Planning Handbook (FSH 1909.12, ch. 10, § 12.52b(3) and (4)), the Responsible Official must document the BASI used in identifying SCC. According to Planning Handbook (FSH 1909.12, ch. zero code, § 07.15), “citations should be one of the principal methods to show how the BASI was applied to the issues being considered.” The actual documents Responsible Official consulted to identify SCC must be referenced and available for public review. For each species considered and rejected, there should be at least one additional source of information referenced that indicates no substantial risk, and the regional forester must document “what information is most accurate, reliable and relevant” to the potential SCC determination in accordance with 36 C.F.R. §219.3. The process does not preclude staff professional judgment, but such judgment must be referenced and discussed in the same manner as other sources.

All Regional Forester Sensitive Species (RFSS) should be identified as potential SCC. The Forest Service classified RFSS as sensitive because their “population viability is a concern” (FSM 2670.5). In the Preamble to the Planning Rule, the Forest Service stated that SCC are similar to existing RFSS because population viability is a concern in each case (77 Fed. Reg. 21216).

The Responsible Official must consider the effect of broad-scale risk factors relevant to the plan area in the potential SCC identification process. The Planning Handbook (FSH 1909.12, ch. 10, § 12.52d(2)(a)) states that, “Species with NatureServe G/T1 or G/T2 status ranks are expected to be included (as SCC) unless it can be demonstrated and documented that known threats for these species, such as those threats listed for the species by NatureServe, are not currently present *or relevant* in the plan area.” In addition, § 12.52(f)(1) recognizes that SCC identification may be warranted by “stressors on *and off* the plan area.” When any source of SCC information suggests that a species is vulnerable in an area that includes the plan area, the Responsible Official must “determine what information is the most accurate, reliable, and relevant to” the persistence of the species in the plan area, in accordance with 36 CFR § 219.3 and use that to demonstrate that the factors outside of the plan area are not relevant to populations in the plan area, and that there is not substantial concern for their persistence in the plan area.

The Responsible Official should include for consideration species that have a NatureServe rank of S3 (state vulnerable). Though the Planning Handbook § 12.52d does not include the S3 ranking as a category that should be *considered*, a “vulnerable” ranking represents a scientific conclusion that there is a regional concern about long-term persistence.

2. Complying with relevant planning rule requirements

a) The plan amendment must “provide for social, economic, and ecological sustainability” as required by 36 C.F.R. § 219.8.

(1) Ecological sustainability and integrity

The Planning Rule requires that plan components “maintain or restore the ecological integrity of terrestrial and aquatic ecosystems and watersheds in the plan area” (36 CFR § 219.8(a)). The first step for assessments in the Planning Handbook is “Identifying the Ecosystems to Assess” for ecological integrity (FSH 1909.12, ch. 10, § 12.11). Compliance with the requirement for integrity of ecosystems cannot be determined without identifying the relevant ecosystems.

The Scoping Document lists a need for the amendment to refocus Management Area 3.63 management “to emphasize rangelands with short-stature vegetation” (Scoping Document: 7). The Proposed Action, summarized in the Scoping Document states, “[w]here possible, adopt use of the Natural Resources Conservation Service’s Ecological Site Descriptions in management area 3.67 as the basis to describe plant communities, evaluate current and desired conditions, and maintain or improve native vegetation and wildlife habitat.” (Scoping Document: 11). What is the definition and description of “rangelands with short-stature vegetation”? This is not clear from the from the list of ecological site descriptions on the Natural Resources Conservation Service’s webpage.[12] As we have recommended elsewhere, the Forest

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[12] Natural Resource Conservation Service. Ecological Site Descriptions. https://www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/ecoscience/desc/.

Service should conduct an amendment assessment. Identifying and describing the ecosystems relevant to the proposed amendment is more appropriately addressed in an assessment *before* the EIS, a primary purpose of which is to disclose a proposed action's (and alternatives') impacts on known affected environment.

We believe it is essential that the Forest Service assess the role of prairie dogs, not only as a species that occurs in the Grassland's grassland ecosystem, but also as a keystone species and ecosystem engineer whose activities are a natural disturbance process for the ecosystem.

(2) Social and economic sustainability

Under the Planning Rule, management plans "must include plan components, including standards or guidelines, to guide the plan area's contribution to social and economic sustainability" (36 C.F.R. § 219.8(b)). In its Scoping Document for the amendment, the Forest Service stated, "[d]espite the ecological significance of prairie dogs, the animals cause widespread and significant concern related to public health, safety of humans and livestock, agricultural production, land values, and facilities" (Scoping Document: 2). The Forest Service must provide evidence, including quantitative data, demonstrating whether these concerns are founded.

Regarding public health concerns, for example, according to the Centers for Disease Control and Prevention (CDC), human plague cases averaged 7 per year between 2000 and 2017 across the United States, with 12 deaths during that time.[13] According to the Wyoming Department of Health, there have been 6 reported human plague cases in Wyoming since 1978.[14] Of course, any human death from a communicable disease is tragic. Yet, contracting plague is an extraordinarily low probability event. Plague, in humans, is treatable with antibiotics. Plague, in prairie dogs, can be prophylactically mitigated, and the current Plan, through the 2015 Management Strategy, specifically directs the Forest Service to do so. But the Forest Service refused to apply preventative measures when plague was first detected on the Grassland in 2017. We seriously question whether the existence of plague warrants the types and extent of management changes proposed by the Scoping Document and Proposed Action—but more importantly, the Forest Service's failures regarding plague mitigation obviate this issue as a valid reason to expend significant resources amending the plan, rather than correctly implementing existing direction.

b) The plan amendment must provide for the diversity of plant and animal communities as required by 36 C.F.R. § 219.9.

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[13] Centers for Disease Control and Prevention, Plague. https://www.cdc.gov/plague/maps/index.html.

[14] Wyoming Department of Health, Infectious Disease Epidemiology Unit. https://health.wyo.gov/publichealth/infectious-disease-epidemiology-unit/disease/plague/.

(1) Ecosystem plan components to maintain or restore ecological integrity and ecosystem diversity (36 C.F.R. § 219.9(a))

The Planning Rule's requirement to develop plan components that maintain or restore ecological integrity requires the Forest Service to carefully consider the importance of parts of Thunder Basin for their value for wildlife and at-risk species. Specifically, Management Area 3.63 contains "ecological conditions, habitats, [and] key ecosystem characteristics…that are unique, under-represented, or rare across the broader landscape" (FSH 1909.12 ch. 20 § 23.11b)—namely the ability to achieve conditions necessary to support a wide-range of prairie dog associated species, including the reintroduction of a viable population of at least 100 breeding black-footed ferrets.

To develop the land management plan consistent with maintaining ecosystem diversity, the plan must include plan components, including standards or guidelines, designed to maintain, restore, or promote ecosystem diversity and habitat types. Moreover, when developing plan components for ecosystem diversity, the Forest Service should pay close attention to Thunder Basin's ability to contribute to the recovery of black-footed ferret and other at-risk species (FSH 1909.12 ch. 20, § 23.11d).

(2) The need for species-specific plan components (36 C.F.R. § 219.9(b))

Managing selected ecosystem characteristics for the diversity and integrity of ecosystems may not sustain populations of all native plant and animal species. The rule therefore requires species-specific plan components, if necessary, to provide the ecological conditions necessary to meet the various conservation requirements for individual at-risk species (36 C.F.R. § 219.9(b)). Together, ecosystem plan components and the species-specific plan components should provide ecological conditions to meet the NFMA requirement for diversity of plant and animal communities.

(a) The plan amendment must "contribute to the recovery of federally listed threatened and endangered species."

The Endangered Species Act requires federal agencies to, "utilize their authorities in furtherance of the purposes of [the ESA] by carrying out programs for the conservation[15] of endangered species and threatened species" (16 U.S.C. § 1536(a)(1)). (See Section VIII on ESA compliance.) NFMA, the Planning Rule, the planning process, and resulting management plans all shape the contours of the Forest Service's authorities that must be marshalled in the service of recovering listed species. Specifically, the 2012 Planning Rule establishes an affirmative regulatory obligation that forest plans "provide the ecological conditions necessary to: contribute to the recovery of federally listed threatened or endangered species" (36 C.F.R. § 219.9(b)(1)). As discussed in Section VI.A above, this planning

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[15] "Conservation" is defined by the ESA to mean "the use of all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to this Act are no longer necessary."

regulation supports NFMA's "diversity requirement." The development of forest plans that contribute to the recovery of listed species and reflect science-based conservation decisions is required to comply, not only with the ESA[16], but with NFMA as well.

(b) The plan amendment must maintain viable populations of SCC

As discussed above, an amended plan must protect potential species of conservation concern the same as designated species of conservation concern would be if they had been designated for the plan area. This means if there is any concern about whether the ecosystem plan components are inadequate to address a potential SCC's risk factors, then the responsible official must ensure the plan contains species-specific components (including standards or guidelines) to address those risk factors. See 36 C.F.R. § 219.9(b); FSH 1909.12 ch. 20, § 23.13. Importantly, a viable population is one "that continues to persist over the long term with sufficient distribution to be resilient and adaptable to stressors and likely future environments." 36 C.F.R. § 219.19. In evaluating this issue, the Forest Service must consider effects of actions outside the plan area in addition to those within the plan area.

c) The plan amendment must provide for ecosystem services and multiple uses as required by 36 C.F.R. § 219.10.

The Forest Service must describe and document the ecosystem services prairie dogs provide for the mixed-grass prairie ecosystem of the Grassland. Along with creating and maintaining habitat for a great diversity of species, prairie dog colonies and colony complexes provide a range of other ecosystems services.

VII. Compliance with the National Environmental Policy Act

The National Environmental Policy Act ("NEPA") has two objectives: (1) it requires an agency "to consider every significant aspect of the environmental impact of a proposed action"; and (2) "it ensures that the agency will inform the public that it has indeed considered environmental concerns in its decisionmaking process." *United States v. Coal. for Buzzards Bay*, 644 F.3d 26, 31 (1st Cir. 2011) (internal citations omitted). Stated another way, NEPA requires federal agencies to take a hard look at the environmental consequences of their actions before they act (See 42 U.S.C. §§ 4321, 4332(2)(C); 40 C.F.R. §§ 1501.2, 1502.25). The key element of this analysis is to evaluate the direct, indirect, and cumulative impacts—also referred to as effects—of several alternatives, including the proposed action, to determine whether an alternative with more conservation potential is available (See C.F.R. §§ 1502.16(a)-(b), 1502.25(c), 1508.16, 1508.27(b)(7)).

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[16] The preamble to the planning rule specifically links this requirement to its responsibility under the ESA for recovery of listed species, stating, "[t]hese requirements will further the purposes of § 7(a)(1) of the ESA, by actively contributing to threatened and endangered species recovery and maintaining or restoring the ecosystems upon which they depend" (77 Fed. Reg. 21215).

The proposed amendment, detailed in the Proposed Action, delineates "major federal actions significantly affecting the quality of the human environment," and accordingly the Forest Service must prepare an EIS (42 U.S.C. § 4332(2)(C)). The Forest Service has committed to preparing an EIS, and we agree with this decision. Below we address additional duties of the Forest Service to ensure that it complies with NEPA.

A. The Forest Service must base its decisionmaking on the best available science.

The Scoping Document and Proposed Action reflect decisionmaking that is not based on sound science, which we have demonstrated in these comments (see Section VIII, for example). Federal agencies are required under NEPA to use "high quality" information in planning (40 C.F.R. § 1500.1(b)). The EIS is the primary vehicle for informing the planning process about the effects of plan components, and NEPA has its own requirements for scientific integrity of the discussions and analysis in environmental impact statements, including references to sources relied upon for conclusions in the EIS (40 CFR 1502.24). Also important, however, is that the Forest Service has incorporated the requirement to use best available scientific information into its NEPA obligations (FSH 1909.12, ch. zero code, § 7.11b).

Forest Service planning regulations require the use of best available scientific information to inform the planning process (see Section VI on NFMA). The December 2016 amendment to the Planning Rule added language to 36 CFR § 219.3 clarifying that the best available scientific information requirement applies to the plan amendment process (81 Fed. Reg. 90729). Compliance with the rule requires two tasks: the Responsible Official (1) "shall determine what information is the most accurate, reliable, and relevant to the issues being considered" (the definition of "best available"), and (2) document the "*basis* for that determination" (36 CFR § 219.3 (emphasis added)).

NEPA serves to protect the environment by ensuring "clarity and transparency" to federal decisions affecting the environment. *N.C. Wildlife Fed'n v. N.C. Dept. of Transp.*, 677 F.3d 596, 603 (4th Cir. 2012). Thus, it is critical that the information the Forest Service uses as a basis for its conclusions in the EIS be disclosed there. This is especially true for the effects on at-risk species. In particular, the Forest Service has a burden of proving assertions important to selection of alternatives.

Throughout these comments and appendices, we have presented much of the best available science that the Forest Service must strongly consider and incorporate into its analyses. Defenders and WWF are experts in black-footed ferret recovery and longtime Executive Committee members of governing body for ferret recovery, the USFWS's Black-footed Ferret Recovery and Implementation Team. PDC is an expert is restoring ferret habitat through prairie dog translocation. Again, as we request elsewhere and detail in Section IX, we strongly recommend the Forest Service conduct an amendment assessment. An assessment will be helpful for developing the effects analysis in the EIS, and most or all the information supporting that analysis should be provided in the assessment. The use of assessments, similar to transparency from the Forest Service, could increase trust in and the public's perception of the planning process.

B. The Forest Service must thoroughly consider alternatives and particularly the no-action alternative.

An evaluation of alternatives to the propose action is vital to an agency's informed decisionmaking and a core goal of NEPA (40 C.F.R. § 1502.1). Indeed, it is "the heart of the environmental impact statement" (40 C.F.R. § 1502.14). The EIS must "[r]igorously explore and objectively evaluate all reasonable alternatives" including "the alternative of no action" (40 C.F.R. § 1502.14(a)&(d)). Every alternative must be given "substantial treatment . . . in detail . . . so that reviewers may evaluate their comparative merits" (40 C.F.R. § 1502.14(b)).

As part of the requirement that the agency consider alternatives, NEPA and Council on Environmental Quality regulations mandate that the agency consider a no-action alternative in all environmental reviews (42 U.S.C. § 4332(2); 40 C.F.R. § 1502.14(d)). This alternative must be based on accurate and robust baseline data and describe the exceptional values of the Grassland for biodiversity and wildlife conservation, prairie dog and prairie dog associated species protection, potential as a ferret recovery site, and potential importance to national ferret recovery. Without a thorough and accurate description of the affected environment, there is simply no way to determine what effect the proposed amendment will have, and, consequently, no way to comply with NEPA (40 C.F.R. § 1502.15). Moreover, to meet Forest Service's NEPA obligations, consideration of the no-action alternative must be vigorous and far-reaching. Such consideration would involve closely analyzing impacts—including beneficial impacts—on prairie dogs, associated species, and the prospects for black-footed ferret recovery.

As we discussed above, the current management plan for the Grassland has not been fully or properly implemented. And we urge the Forest Service to select the no-action alternative as its preferred alternative for the DEIS. To be fully clear, we do not support the proposed action alternative—or any alternative that would further weaken protections for prairie dogs and associated species, or the potential to establish a ferret population as outlined in the current Management Plan.

C. The Forest Service must analyze and fully disclose in the EIS the adverse impacts of the proposed amendment to the grassland ecosystem and numerous wildlife species.

An EIS must take a hard look at the direct, indirect, and cumulative effects of the proposed amendment on the human environment as well as means to mitigate adverse environmental impacts, including ecological impacts (40 C.F.R. §§ 1502.16, 1508.25(c)). The EIS for the proposed amendment must evaluate the effects in a way that will meaningfully inform decisionmakers and the public about likely outcomes. Stated another way, the effects analysis needs to be more than a subjective, qualitative, and comparative analysis—it requires in-depth analyses of significant issues (40 CFR §1501.7(a)(2)), such as species viability requirements. Below is a non-exhaustive list of topics and issues that should be thoroughly analyzed and considered in the EIS:

- The analysis must detail how specific proposed plan components affect each ecological condition needed by at-risk species. It is fundamental that the EIS properly characterize what the plan components direct the Grassland to do.
- The EIS analysis must properly account for the effects of removing protective standards from the current plan. Some plans seem to have a core assumption that more flexibility is good, and therefore that standards should be limited. Standards provide greater certainty that activities having adverse effects will not occur, though we do not support the proposed standard modifications, removals, and additions in the Proposed Action.
- The Forest Service must also address broad-scale effects during management planning. Cumulative effects can include all factors "beyond the authority of the Forest Service" (36 CFR § 219.9(b)(2)) including activities of state and local entities that impact wildlife and biodiversity in the region.
- The EIS must also disclose and address uncertainty and risk. NEPA requires disclosure of incomplete or unavailable information (40 CFR § 1502.22). For at-risk species, it is especially important to characterize the level of uncertainty and the effects in terms of how plan components increase or decrease risk.

D. The Forest Service must conduct a Biological Evaluation for each threatened or endangered species, Regional Forester Sensitive Species, and potential Species of Conservation Concern likely to be affected by the amendment.

The Forest Service should follow national-level direction (FSM 2600, ch. 2670, 2005) and Regional 2 direction (FSM 2600, ch. 2670, 2018) for developing biological evaluations. Species that must be evaluated in the biological evaluation include the following, at minimum: black-footed ferret; black-tailed prairie dog, species associated with prairie dogs—mountain plover, burrowing owl, swift fox, ferruginous hawk, and others; all Regional Forester Sensitive Species, all potential Species of Conservation Concern.

Additionally, to meet the Planning Rule requirements, as guided by FSH 1909.12, ch. 10, § 12.14a, the Forest Service must describe the natural range of variation of prairie dog disturbance across the landscape. The DEIS must determine the effects of setting the limits on prairie dog colony acreage and distribution described by the Scoping Document and Proposed Action. This information must be included in the biological evaluation.

VIII. Compliance with other applicable laws

A. The amendment must comply with the Endangered Species Act.

The black-footed ferret was one of the first species in the United States designated as endangered by U.S. law. It was first listed under the Endangered Species Preservation Act of 1966 (32 Fed. Reg. 4001, 4001 (Mar. 11, 1967) and has remained listed ever since. The species is currently designated endangered under the Endangered Species Act of 1973. 50 C.F.R. § 17.11(h) (current list of endangered and threatened wildlife).

Five black-footed ferret sightings were documented on Thunder Basin between 1971 and 1977 (USFS, MBNF & TBNG 1985). The last ferret was observed on the Grassland in 1981 (USFS, MBNF & TBNG 1985).

Though black-footed ferrets do not currently occupy Thunder Basin National Grassland, the Forest Service is nonetheless obligated under the ESA to promote their recovery. Congress enacted the ESA to provide "a program for the conservation of . . . endangered species and threatened species" (16 U.S.C. § 1531(b)). Section 2(c) of the ESA establishes that it is "the policy of Congress that all Federal departments and agencies shall seek to conserve endangered species and threatened species and shall utilize their authorities in furtherance of the purposes of this Act" (16 U.S.C. § 1531(c)(1)). Section 7(a)(1) of the Act mandates that federal agencies "utilize their authorities in furtherance of the purposes of this Act by carrying out programs for the conservation of endangered species and threatened species" (16 U.S.C. § 1536(a)(1)). The ESA defines "conservation" to mean "the use of all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to this [Act] are no longer necessary" (16 U.S.C. § 1532(3)).

The current (Donald R. (Pete) Gober) and former (J. Michael Lockhart) USFWS Black-footed Ferret Recovery Program coordinators have long noted the importance of federal land management agencies complying with Section 7(a)(1) of the ESA to promote ferret recovery, stating in 2006,

> Federal public lands (national grasslands, Bureau of Land Management property, national wildlife refuges, national parks and monuments, and military lands) should bear a disproportionate amount of habitat development. Responsibilities under section 7(a)(1) of the ESA (a provision requiring all Federal agencies to fully promote and support endangered species recovery) should be reinforced at the national level, both with funding and refocused priority, to establish and manage large prairie dog complexes wherever possible. (Lockhart et al. 2006: 18)

The USFWS recently affirmed the importance of Thunder Basin for this recovery effort:

> TBNG is one of the few large grassland properties with extensive black-tailed prairie dog populations and accordingly is of particular interest as a site that has extremely high potential to contribute to the recovery of the endangered black-footed ferret (ferret). In fact, TBNG may well be the best existing potential site across the species' range in 12 western states, Mexico, and Canada that could significantly contribute to ferret recovery at the present time. [17]

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[17] United States Department of Interior, U.S. Fish and Wildlife Service. 2017. Letter to Mr. Brian Ferebee (Regional Forester, U.S. Forest Service, Rocky Mountain Region) from Ms. Noreen E. Walsh (Regional Director, U.S. Fish and Wildlife Service, Mountain-Prairie Region). May 30.

The USFWS's black-footed ferret recovery delisting objectives (USFWS 2013: 6, 62) are to:

- Establish ≥3,000 free-ranging breeding adult black-footed ferrets in 30 or more populations, with at least one population in each of at least 9 of 12 States within the historical range of the species, with no fewer than 30 breeding adults in any population, and at least 10 populations with 100 or more breeding adults.

- Maintain these population objectives for at least three years prior to delisting.

Notably, there are few sites in the ferret's range with sufficiently large prairie dog complexes to support 100 adult ferrets. In 2007, at the peak of ferret populations in the wild, there were only five reintroduction sites that hosted, or had the near potential to host, 100 breeding adults.[18] Today, there are no reintroduction sites with 100 breeding adults due to sylvatic plague and drought conditions. Although efforts are underway to increase ferret numbers at the five sites that were nearing 100 breeding adults in 2007, five additional sites capable of hosting 100 breeding adult ferrets are needed to achieve delisting objectives.[19] Ensuring that Thunder Basin National Grassland is one of those five sites is essential to ferret recovery. Adoption and implementation of this proposed amendment will preclude recovery of the species.

Thunder Basin has been considered a promising black-footed ferret recovery site for decades. However, the proposed amendment indicates the Forest Service is abandoning its long-standing efforts to honor its Section 7(a)(1) obligation. Since at least 1985—and until the current proposed amendment—the Forest Service has developed and implemented management prescriptions, administered projects, and undertaken other actions to provide the conditions necessary for black-footed ferret recovery and reintroduction on Thunder Basin.

The Forest Service has consistently and specifically protected prairie dog colonies to provide habitat for ferret reintroduction. As scientific understanding of the prerequisites to successful black-footed ferret reintroduction has been refined, the Forest Service's actions on Thunder Basin related to ferrets centered around implementing greater protections of prairie dogs over larger portions of the Grassland to expand prairie dog colonies to facilitate ferret recovery. This is evident from the Forest Service's Biological Assessment (BA) for the 1985 management plan, which recognizes the need to protect potential, though currently unoccupied, black-footed ferret habitat:

> Prairie dog towns are considered the primary black-footed ferret habitat providing a year around food source and shelter (Hillman 1968, Henderson et al. 1969, Linder et.al. 1972). Prairie dog town mapping activities on the Grassland during 1979 through 1984 have indicated

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[18] BFFRIT (Black-footed Ferret Recovery Implementation Team) Conservation Subcommittee, 2019. BFF [black-footed ferret] Site Estimates 2018, Table. Presented at April 10, 2019 meeting, Fort Collins, Colorado.

[19] BFFRIT (Black-footed Ferret Recovery Implementation Team) Conservation Subcommittee, 2019. BFF [black-footed ferret] Site Estimates 2018, Table. Presented at April 10, 2019 meeting, Fort Collins, Colorado.

> approximately 100 prairie dog towns totaling 13,046 acres to be located on Forest Service administered lands. All these prairie dog towns can be considered potential black-footed ferret habitat. (USFS, MBNF & TBNG 1985: G-7)

In turn, the 1985 management plan specifically identified land areas of the Grassland to focus on prairie dogs and ferret reintroduction. The Final Environmental Impact Statement for the Medicine Bow National Forest and Thunder Basin National Grassland Land and Resource Management Plan of 1985 plan stated, "[a]pproximately 2,240 acres of prairie dog towns have been identified as potential habitat for the black-footed ferret. These areas are managed for black-footed ferret habitat …" (USFS, MBNF & TBNG 1985: III-46). The 1985 management plan also designated the black-footed ferret a "recovery species."

Notably, the 1985 plan was finalized before the 1988 Black-footed Ferret Recovery Plan recovery criteria were developed. Yet the USFWS's Biological Opinion (BO) for the 1985 plan demonstrates that the Service fully expected that the Forest Service would continue managing and protecting prairie dogs, despite the absence of ferret occupancy, to prepare for future reintroduction:

> Our concurrence of "no affect" [*sic*] on the black-footed ferret is based on established and continuing Forest Service commitments to the Thunder Basin Prarie [*sic*] Dog Management Plan which provides guidance on conducting surveys for ferrets on prairie dog towns for management actions or other disturbance proposals. In addition, the Forest Service is commited [*sic*] to maintaining a potential 5400 acres of prairie dog towns with about 2240 of these towns identified as "potential" ferret habitat. … We encourage research on the dynamics of the prairie dogs on the Grassland in order to help develop management plans for prairie dog town complexes used for ferret reintroduction projects in the future. (USFS, MBNF & TBNG 1985: G-2)

Subsequent annual monitoring reports for the 1985 management plan indicate the Forest Service was tracking potential ferret habitat on the Grassland. For example, the 1998 monitoring report, stated, "[h]abitat capability is summarized as increasing for: bald eagle, black-footed ferret, black-tailed prairie dog, and Mountain plover" (MBNF 1998: unpaginated).

By 2001, the scientific understanding of what constitutes high quality ferret habitat and what minimum prairie dog complex sizes are needed to support viable ferret populations evolved. In a letter from (then) USFWS ferret recovery coordinator, Mike Lockhart to Bob Luce (black-tailed prairie dog interstate coordinator), dated March 16, 2001, Mr. Lockhart states:

> … the only true measure of ferret reintroduction success to date suggests that high density, plague-free, black-tailed prairie dog complexes in excess of 10,000 acres, with large core colonies, and which are not subject to artificial perturbations (e.g., shooting/poisoning) are needed to reestablish wild ferret populations. Conversely, ferret reintroductions into smaller,

> more isolated, prairie dog complexes, have not successfully established stable ferret populations, even in complexes with relatively high prairie dog densities.[20]

In line with Mr. Lockhart's expert recommendations, Thunder Basin National Grassland's 2001 Land and Resource Management Plan designated the 3.63 Management Area for "Black-footed Ferret Reintroduction Habitat," and prioritized that, "[b]lack-tailed prairie dog colony complexes are actively and intensively managed as reintroduction habitat for black-footed ferrets" (USFS, TBNG 2001: 3-16).

Consistent with the Forest Service's Section 7(a)(1) obligations, the 2001 LRMP also prescribed the desired condition that "[l]arge prairie dog colony complexes are established and maintained as suitable habitat for black-footed ferret reintroductions. Land uses and resource management activities are conducted in a manner that is compatible with maintaining suitable ferret habitat" (USFS, TBNG 2001: 3-16). Furthermore, the Forest Service did not consider landowner resistance a prompt to abandon the aim of the Grassland to serve as a ferret recovery site, but rather to find workable alternatives:

> The Forest Service works with other agencies and organizations to pursue conservation agreements or easements with adjoining land jurisdictions to achieve black-footed ferret recovery objectives. Where landownership patterns are not conducive to effective and successful prairie dog and black-footed ferret management, landownership adjustments with willing landowners may also be used to help resolve management issues. (USFS, TBNG 2001: 3-16)

The 2001 LRMP also included strict standards to protect the 3.63 Management Area such as conditions on the use of rodenticides and direction to prohibit shooting within ferret reintroduction habitat. (USFS, TBNG 2001: 3-17).

In 2001, the Forest Service banned shooting on 72,500 acres of prairie dog habitat on Thunder Basin (Matthews et al. 2001).[21] Buseck et al. (2005: 25) stated, "[t]his ban is one of the first of its kind on public lands." The shooting restrictions were intended "to allow populations to expand in anticipation of black-footed ferret reintroduction" (Buseck et al. 2005: 35).

More recently, Luce (2006), at the time recently retired from the Wyoming Game and Fish Department, listed Thunder Basin as one of three "immediate potential sites" for black-footed ferret recovery. Luce (2008) conducted an inventory of potential ferret recovery sites across the species historic range and again included Thunder Basin in his list of potential sites. Luce (2008: 36) noted the positive potential for intra-jurisdictional land units to coordinate ferret recovery, stating,

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[20] Letter from Mr. J. Michael Lockhart (USFWS, Black-footed Ferret Recovery Coordinator) to Mr. Bob Luce (Black-tailed Prairie Dog Interstate Coordinator. March 16, 2001.

[21] In 2010, the Forest Service expanded the shooting area closure from 72,500 acres to 100,460 (USFS, TBNG 2014).

> Entities within the same jurisdiction such as Wind Cave, Badlands, and Theodore Roosevelt National Parks should consider the individual parks as components of a mega-reintroduction site. National Grasslands, including Thunder Basin, Little Missouri, Cimarron, Kiowa, Comanche, Pawnee, and others could function similarly within the U.S. Forest Service. This approach would facilitate interchange of management approaches and translocation of black-footed ferrets between sites.

Prior to a plague outbreak in 2001, about 18,000 acres of occupied prairie dog colonies occurred on the Grassland, and close to 20,000 acres in the region with the inclusion of state lands in the count (Luce 2008).

After a long-term stakeholder effort, the Forest Service implemented Amendment #3 to the 2001 LRMP. Though the Forest Service modified Management Area 3.63 and prairie dog management tools to enhance community support, Amendment #3 to the 2001 LRMP reiterated that Thunder Basin would serve as a ferret reintroduction site, and the Forest Service would protect and manage a sufficient area of active prairie dog colonies to meet the USFWS's recovery plan objectives. As stated in the Record of Decision for Amendment #3 of the Management Plan,

- The Category 1 Prairie Dog Habitat has a management objective of at least 18,000 acres of active prairie dog colonies. The acreage in Category 1 is not capped at 18,000 acres but would be allowed to grow within the boundary of the Management Area 3.63. (USFS, TBNG 2009: 3)

- Any prairie dog control efforts to address unwanted colonization onto non-federal lands within Category 1 Prairie Dog Habitat proposing to use rodenticides may only be initiated if cumulative acreage of active prairie dog colonies within Category 1 exceeds 18,000 acres. (USFS, TBNG 2009: 4)

- Category 1 Prairie Dog Habitat will be considered core habitat. Recreational shooting of prairie dogs will be prohibited year-round within Category 1 Prairie Dog Habitat. (USFS, TBNG 2009: 3)

In short, facilitating the reintroduction (and recovery) of black-footed ferrets has long been a Forest Service goal on Thunder Basin—one that is integral to ensuring that the Forest Service is complying with its Section 7(a)(1) obligations.

By 2017, in response to complaints by a few landowners and lessees to state and federal officials in Wyoming regarding prairie dog management on the Grassland, the Forest Service began signaling its change in direction and abdication from managing the Grassland in a way that complies with Section 7(a)(1) of the ESA. Communications make clear the Forest Service is acquiescing to political pressure to weaken prairie dog conservation measures intended to provide ferret suitable habitat. On May 19, 2017, Regional Forester Ferebee of the Rocky Mountain Region of the Forest Service sent a letter to the Wyoming County Commissioners Association, with a copy to Governor Mead, outlining a list of actions the Forest Service would take that would detrimentally impact progress toward ferret recovery: prohibit plague mitigation, increase prairie dog poisoning, and explore the use Rozol[22] (Ferebee, USFS 2017). In response, we (Defenders of Wildlife, Prairie Dog Coalition of the Humane Society of the United States, and World Wildlife Fund) communicated our concerns in a series of letters and in-person meetings to the Forest Service (and others). Except for anticoagulant use to which the Forest Service will not permit, these concerns have not been alleviated.

More recent statements and letters also illustrate the agency's recent aversion to complying with ESA mandates. A December 4, 2017 Interagency Statement (USFS, MBRNF & TBNG et al. 2017) between Forest Service, USFWS, and Wyoming Game and Fish Department declared,

> We cooperatively agree that the reintroduction of black-footed ferrets on the Grassland is not appropriate at this time. Instead, the current focus surrounds prairie dog management actions, including boundary control and disease control. The U.S. Forest Service will monitor ecological progress and grassland restoration activities on the Grassland. Interaction with stakeholders will continue on these important issues.[23]

With no clear grounding in science, law, or policy, political pressure from Wyoming government leaders seems to have influenced the Forest Service. On December 3, 2018, the Select Federal Natural Resource Management Committee of the Wyoming Legislature (2018), represented by co-chairs Senator Michael Von Flatern and Representative Tyler Lindholm, sent a letter to the WYGD, Forest Service (Rocky Mountain Region), and USFWS (Mountain-Prairie Region),

> We strongly urge your agencies to not include the Grassland as a potential reintroduction site for black-footed ferrets in any future memorandum of understanding or interagency agreement. There are several issues that must be resolved before reintroduction, including boundary control, dedicated funding for boundary and plague control, and the lack of support from landowners adjacent to the Grassland and in surrounding areas. We also believe that it would be prudent to delay considering the Grassland as a reintroduction site until the Thunder Basin National Grassland Land and Resource Management Plan is amended to allow for better management of the prairie-dog population. In materials provided to the Committee in September, the Wyoming Game and Fish Department, the Wyoming Department of Agriculture, the United States Forest Service, and the United States Fish and Wildlife Service stated that they do not support ferret reintroduction on the Grassland until these issues are resolved.

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[22] Rozol is an anticoagulant toxicant believed to be more effective at killing prairie dogs than other rodenticides, like zinc phosphide, but it also comes with a greater risk of killing non-target predators that eat poisoned prairie dogs. (*See* Letter from Regional Director Noreen Walsh, USFWS, to Regional Forester Brian Ferebee, USFS (May 30, 2017)). At Footnote #1.

[23] The existing management plan contains robust provisions to ensure adequate boundary and disease control to address local concerns, but the Forest Service has repeatedly failed to use them. (See Section III above).

Despite the Wyoming Select Committee's letter that suggests resolving landowner conflicts, the Scoping Document for the amendment and the Proposed Action propose stripping current plan direction to work with landowners to progress toward ferret recovery.

That the Forest Service is acting on politics and landowner interests rather than science or law is evident throughout the Scoping Document. The Forest Service is proposing to replace the designated ferret reintroduction habitat on Thunder Basin with a focus on "rangelands with short-statured vegetation" that allows prairie dog area reductions, by lethal and other means, when the total active prairie dog acres exceeds 7,500, with exceptions to also allow for reductions when below 7,500 as well as blanket approval for "density control" (or scattered poisoning throughout) at any time (Scoping Document: 11). The agency further proposes that active prairie dog colonies "be distributed across the landscape and vary in size, up to approximately 1,000 acres, with an emphasis on colonies of 100 to 400 acres," with at least one colony complex to "be managed for at least 1,500 acres of active prairie dog colonies" (Scoping Document: 11).

The goal of managing for the very minimum size of active colonies to allegedly support associated species meets no credible best available science threshold for supporting a viable black-footed ferret population—especially where these colonies are fragmented across the management area and face persistent shooting and poisoning. Moreover, the Forest Service has not provided a scientific basis supporting its proposed emphasis on 100- to 400-acre colonies. Although the USFWS suggests 1,500 acres as a minimum for consideration to begin a ferret reintroduction effort into black-tailed prairie dog colonies in its Safe Harbor Agreement, that number is well below the size of colonies supported by science in the recovery plan as well as empirical evidence at Conata Basin necessary to sustain a population (USFWS 2013). Moreover, there is no 1,500-acre recovery site in North America today that hosts or is even capable of hosting the required 30 breeding adults to count towards downlisting or delisting the species.[24]

The Scoping Document (p. 7) includes the following need statement in the Purpose and Need section:

> Ensure management direction identifies habitat requirements needed to support viable populations of prairie dogs and associated species, such as mountain plover, burrowing owl, and swift fox, and that management would ***not preclude future reintroduction of black-footed ferret***. (emphasis added)

"Not preclude" is significantly different than "conserving," as defined in the ESA, or "recovering," and does not meet the spirit and mandate of Section 7(a)(1) of the ESA. The Forest Service proposed amendment will not meet the minimum requirements for managing adequate ferret recovery habitat or establishing a ferret population that will contribute to federal recovery objectives or persist into the foreseeable future.

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[24] BFFRIT (Black-footed Ferret Recovery Implementation Team) Conservation Subcommittee, 2019. BFF [black-footed ferret] Site Estimates 2018, Table. Presented at April 10, 2019 meeting, Fort Collins, Colorado.

Moreover, the proposed amendment likely does not even meet the Forest Service's baseless "not preclude" standard. If the proposed amendment will support viable populations of prairie dogs at all, those populations will be small, fragmented, and likely routinely subject to poisoning, shooting and harassment, and potential extermination due to plague. Without robust and resilient prairie dog populations, there will be no opportunity to successfully recover ferrets to Thunder Basin. The loss of Thunder Basin as a reintroduction site must be further viewed through the lens of black-footed ferret recovery as a whole. Delisting the ferret will require at least 10 populations with 100 or more breeding adults, and—as the USFWS acknowledges—Thunder Basin is one of only a few sites on federal lands with the potential to support that size population.[25]

Thunder Basin's 1985 and 2001 management plans, including Amendment #3, and the 2015 Black-tailed Prairie Dog Conservation Assessment and Management Strategy for the Thunder Basin National Grassland all maintain the expectation that ferrets would be reintroduced to the Grassland. The Forest Service has dedicated close to 35 years preparing the Grassland for ferret recovery by managing prairie dogs at numbers that would allow for the species to return to the Grassland. By abandoning the 3.63 Management Area designation and plan standards meant to protect prairie dog habitat specifically for ferret recovery, the proposed amendment would break not only precedent, but the law.

B. The amendment must comply with the Migratory Bird Treaty Act.

The Forest Service must comply with the Migratory Bird Treaty Act (MBTA) in the development of the amendment (16 U.S.C. §§ 703-712). The Grassland is part of the breeding range for least 16 migratory birds protected by the MBTA (IPaC, accessed May 11, 2019) (see table below). The MBTA makes it unlawful "at any time, by any means or in any manner, to pursue, hunt, take, capture, kill, attempt to take, capture, or kill, [or] possess . . . any migratory bird" unless otherwise permitted by regulation (16 U.S.C. § 703). Any take or kill of migratory birds on the Grassland without authorization would violate the MBTA.[26] The Forest Service must address how it will ensure compliance with the MBTA in relation to the proposed amendment in the DEIS.

Migratory Bird Species	Breeding Season	USFWS Bird of Conservation Concern
Bald Eagle	Dec 1 to Aug 31	

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[25] United States Department of Interior, U.S. Fish and Wildlife Service. 2017. Letter to Mr. Brian Ferebee (Regional Forester, U.S. Forest Service, Rocky Mountain Region) from Ms. Noreen E. Walsh (Regional Director, U.S. Fish and Wildlife Service, Mountain-Prairie Region). May 30.

[26] The validity of the Department of Interior's recent attempt to reverse its longstanding interpretation of the MBTA (as reflected in Solicitor Opinion M-37050) is currently under review. *See Nat'l Audubon Society v. U.S. Dept. of the Interior*, 18-cv-04601 (S.D.N.Y. filed May 24, 2018). The reversal is at odds with multiple court rulings regarding the application and enforcement of the MBTA. *See, e.g., U.S. v. FMC Corp*, 428 F.Supp. 615 (W.D.N.Y. 1977), *aff'd*, 572 F.2d 902 (2nd Cir. 1978); *see also* Solicitor Opinion M-37041, "Incidental Take Prohibited Under the Migratory Bird Treaty Act" (Jan. 10, 2017).

Haliaeetus leucocephalus		
Brewer's Sparrow *Spizella breweri*	May 15 to Aug 10	BCC
Burrowing Owl *Athene cunicularia*	Mar 15 to Aug 31	BCC
Chestnut-collared Longspur *Calcarius ornatus*	May 1 to Aug 10	BCC
Clark's Grebe *Aechmophorus clarkii*	Jan 1 to Dec 31	BCC
Ferruginous Hawk *Buteo regalis*	Mar 15 to Aug 15	BCC
Golden Eagle *Aquila chrysaetos*	Jan 1 to Aug 31	BCC
Lark Bunting *Calamospiza melanocorys*	May 10 to Aug 15	BCC
Lesser Yellowlegs *Tringa avipes*		BCC
Long-billed Curlew *Numenius americanus*	Apr 1 to Jul 31	BCC
Marbled Godwit *Limosa fedoa*	May 1 to Jul 31	BCC
Mccown's Longspur *Calcarius mccownii*	May 1 to Aug 15	BCC
Mountain Plover *Charadrius montanus*	Apr 15 to Aug 15	BCC
Pinyon Jay *Gymnorhinus cyanocephalus*	Feb 15 to Jul 15	BCC
Red-headed Woodpecker *Melanerpes erythrocephalus*	May 10 to Sep 10	BCC
Sage Thrasher *Oreoscoptes montanus*	Apr 15 to Aug 10	BCC
Willet *Tringa semipalmata*	Apr 20 to Aug 5	BCC

C. The amendment must comply with the Bald and Golden Eagle Protection Act.

Both bald eagles and golden eagles occur and nest in the Grassland (Gaines 1996). Both species are protected under the Bald and Golden Eagle Protection Act (BGEPA) (16 U.S.C. §§ 668–668c). A permit must be secured for any activities that might take or disturb eagles (50 C.F.R. §§ 22.1–22.32). The Grassland provides habitat for bald eagle and golden eagles persistence. The USFWS has developed national guidelines for managing bald eagles (USFWS 2007). The Forest Service must assess whether and how the proposed amendment might affect eagles.

Bald and golden eagles forage in prairie dog colonies. Prairie dogs are an important food source for golden eagles year-round in the Thunder Basin region and for bald eagles, particularly in winter (Stephens et al. 2005). Both species are known to hunt live prairie dogs and scavenge on dead prairie dog carcasses. Secondary poisoning from consuming poisoned prairie dogs (Rattner et al. 2015), lead poisoning from consuming prairie dogs shot with lead ammunition (Stephens et al. 2005; Pauli and Buskirk 2007) are threats to these species that will increase in risk with increased prairie dog poisoning and shooting on the Grassland. We note that the current Proposed Action indicates the amendment will not authorize anticoagulant poisons, which are known to pose a greater risk of secondary poisoning than other toxicants such as zinc phosphide (Scoping Document: 11). But the ingestion of zinc phosphide, a commonly used rodenticide used to exterminate prairie dogs, can negatively the health of eagles who feed on poisoned rodent carcasses (EPA 2004).

IX. Need for an assessment

We strongly suggest and specifically request that the Forest Service conduct an amendment assessment if it continues to go forward with the amendment process (FSH 1909.12, Ch. 10, § 15). The Scoping Document indicates the Forest Service has not availed itself of new information, particularly new scientific information, to sufficiently evaluate ecological and economic conditions and trends. The Forest Service has not completed a management plan monitoring report since 2012 for the year 2011, and, accordingly, the agency may not fully understand the conditions on the Grassland or possess best available scientific information (BASI) made available in the last 8 years or more.

We are particularly concerned that the Forest Service is proposing an amendment that presents an inappropriate management scheme for the existing ecological conditions on the Grassland. The Scoping Document emphasizes the expansion of “active” prairie dog colonies on and around the Grassland to 75,000 acres. The Forest Service describes this expansion as “more than doubling the previous record for mapped acres” (Scoping Document: 5) and appears to couch this as a problem the amendment is meant to solve. Yet, this expansion—48,000 acres of which occurred on the Grassland, with the remainder on private land—is within the natural range of variation for a prairie dog colony area, especially in the broader landscape context, and was predicted and expected by the Forest Service as outlined in the Biological Assessment and Evaluation (Appendix H) of the 2001 Northern Great Plains Management Plans Revision (USFS 2001). We are concerned the Forest Service does not recognize this.

Most importantly, 75,000 acres of prairie dogs ***is not*** the condition on the Grassland and broader landscape today. The Scoping Document points out that plague took a massive toll on prairie dogs in 2017, reducing active prairie dog colonies in and around Management Area 3.63 to about 1,000 acres, of which about 600 acres is on the Grassland. This is a condition that requires a very different management approach, one that focuses on recovering prairie dog populations to again be sufficient to support a viable ferret population. The Forest Service must assess the ecological effects of prairie dog losses to the landscape and effects on associated species to fill in knowledge gaps indicated by the proposed prescriptions in the Scoping Document and Proposed Action.

The Forests Service makes the following statement in the Scoping Document that the amendment is needed to "[e]nsure management direction identifies habitat requirements needed to support viable populations of prairie dogs and associated species …" (Scoping Document: 7). The statement demonstrates the Forest Service must assess the habitat requirements of these species.

The Forest Service must assess the economic conditions at play on the Grassland. The agency and the public must understand the past and recent trends in and projected costs of rodenticides purchases and use on the Grassland. What is the public interest benefit derived from the Forest Service's investment in this benefit to a private interest?

We urge the Forest Service to follow the guidance for assessments in the Planning Rule under 36 C.F.R. § 219.6(b) to conduct an amendment assessment of the following factors:

- The effects of the loss of prairie dogs to the terrestrial mixed-grass prairie ecosystem that dominates the Grassland and the species that depend on and benefit from prairie dogs as proposed by 36 C.F.R. § 219.6(b)(1) and (5) and associated guidance in the Planning Handbook. Prairie dogs are keystone species and benefit suites of species beyond prairie dog associate species and restore and maintain overall Grassland biodiversity. The Forest Service must assess the benefits of prairie dogs to the ecosystem and grassland species. Additionally, the Forest Service must examine the natural range of variation of occupied prairie dog colony area on the Grassland and the broader landscape.

- The effects of proposed management changes on the ability of prairie dog activity and fire to serve as keystone system disturbance processes—system drivers—on the Grassland proposed by 36 C.F.R. § 219.6(b)(3) and associated guidance in the Planning Handbook. Prairie dogs provide ecosystem services, such as soil moisture retention and improved forage quality and digestibility for livestock and native ungulates. But prairie dogs lose the ability to serve their essential ecosystem engineering role when population numbers and colony area are kept at artificially low levels. Additionally, fire is an essential disturbance process for the Great Plains grassland ecosystem. Proposed changes in management of these ecosystem drivers must be assessed.

- The effects of domesticated livestock as an ecosystem stressor and driver for the Grassland's dominant terrestrial ecosystem as proposed by 36 C.F.R. § 219.6(b)(3) and associated guidance in the Planning Handbook. We accept that livestock grazing will remain a use on the Grassland. But the Forest Service must take the BASI on this topic and assess the effects of livestock grazing on prairie dogs and associated and other species that benefit from prairie dog habitat. For example, Kohl et al. (2013) found that increased grazing and decreased movements by cattle combined with livestock stocking levels supported the hypothesis that current range practices are resulting in homogeneous grazing at a landscape scale and thus contributing to the decline of prairie-obligate species (see also Knopf 1996; Fuhlendorf et al. 2010). The importance of this ecological integrity issue (and also social issue)—prairie dog conservation and livestock grazing operations—to grassland management and conservation should necessitate a thorough scientific review of the literature on the ecological interactions between cattle and prairie dogs.

- A comprehensive assessment of the knowledge on competition and coexistence between cattle and prairie dogs. Prairie dogs can and do co-exist with cattle and contribute to healthy grasslands that provide forage for domestic livestock (see Sierra-Corona et al. 2015). The Forest Service must use the BASI to conduct an assessment that includes consideration of the benefits prairie dogs provide in coexistence with livestock.

X. Identifying and obtaining missing information

We previously requested the documentation the Forest Service relied upon to support several specific statements in the Scoping Document. We believe this information should be disclosed prior to the publication of the Draft EIS and renew our request the Forest Service to promptly make, at minimum, the following information available to the public:

- Roster of Interdisciplinary Team members.

- Documentation of the Forest Service's efforts to minimize impacts of prairie dog encroachment onto private and state lands, i.e., "the good neighbor policy." (see Scoping Document: 4)

- Documentation that prairie dogs are encroaching onto neighboring properties. (see Scoping Document: 4)

- The Forest Service stated in the Scoping Document that mapping efforts between 2015 and 2017 indicated 75,000 acres of active black-tailed prairie dog colonies existed in the vicinity of Management Area 3.63, of which 48,000 acres occurred on the Grassland. Documentation for the method used and the mapping results. (see Scoping Document: 5-6)

- Documentation of economic impacts to neighboring land values. (see Scoping Document: 2)

- Documentation of impacts to agricultural production. (see Scoping Document: 2)

- Best available scientific information documenting that Proposed Action 6b, "Active prairie dog colonies should be distributed across the landscape and vary in size, up to approximately 1,000 acres, with an emphasis on colonies of 100 to 400 acres" is sufficient to support a viable population of black-footed ferrets. (see Scoping Document: 11)

- Best available science documentation that managing for 7,500 acres of prairie dogs will support a viable population of black-footed ferrets, based on proposed Action 6c, "All prairie dog colony management tools not otherwise restricted by the plan will be available for use when the active acreage in management area 3.67 is greater than 7,500 acres." (see Scoping Document: 11)

XI. Conclusion

A thriving grassland ecosystem that maintains an abundance of wildlife and supports sustainable uses by the people who live adjacent to Wyoming's Thunder Basin National Grassland is possible. We believe this is a vision shared with the Forest Service, myriad stakeholders, and the American public who all have a voice for this Grassland. Unfortunately, the Forest Service's proposed amendment will steer away from this vision. It is likely to threaten the viability of prairie dogs and associated species that call the Grassland home. Further, it will not contribute to the recovery of the black-footed ferret.

The proposal's substantial removal of protections for prairie dogs will not change the issue of lack of implementation of the current plan, but it will lead to increased conflict on an issue that has been addressed previously and significantly in multiple public participation processes. The proposed amendment is likely to fail to comply with federal law, would preclude recovery for federally endangered black-footed ferret, and would put other imperiled species at an even greater risk of extinction. For these reasons, and the many others we outline above, we oppose the proposed amendment for Thunder Basin. We reiterate that the policy instruments the Forest Service believes it needs for "balance" remain available in the existing Management Plan.

Our organizations have dedicated substantial amounts of time and resources to promote the protection and recovery of the Grassland's wildlife, while respecting the Forest Service's multiple use mandate. We offer considerable expertise on relevant subjects to the proposed amendment, including black-tailed prairie dog and associated species conservation, black-footed ferret recovery, and national forest and grassland management planning. Given this, we would like to reiterate the following key comments:

- The Forest Service needs to comply with NFMA, National Environmental Policy Act, Endangered Species Act, the Migratory Bird Treaty Act, and the Bald and Golden Eagle Protection Act.
- Retain and fully implement the current plan, including the recovery and maintenance of prairie dog populations and associated species within Management Area 3.63 as it is essential in advancing recovery of the endangered black-footed ferret. Specifically, we request the Forest Service continue to manage toward a prairie dog complex of at least 18,000 acres of active prairie dog colonies in a contiguous area.
- Solutions to facilitating livestock and prairie dog coexistence must center on land uses and resource management activities that are conducted in a manner that is compatible with

maintaining suitable black-footed ferret habitat. Standards listed in the TBNG plan (Chapter 3, Management Area 3.63, General – 1 (revised)) include: 1) *Authorize only those uses and activities that do not reduce the suitability of the area as black-footed ferret reintroduction habitat*; and 2) *Manage all prairie dog colonies within this management area as though they were occupied by black-footed ferrets, and apply all Standards and Guidelines as though black-footed ferrets occur in all colonies*. And these standards must remain intact.

- Conduct annual monitoring of prairie dog populations and vegetation and employ the appropriate decision trees outlined in the current plan to adequately respond to changes that warrant a timely response.
- Repair communication, compromise, and trust among all Thunder Basin stakeholders by improving collaborative efforts that can transform social conflict and create sustainable solutions for people and wildlife. This could result in lasting outcomes related to prairie dog conservation and management on Thunder Basin National Grassland and enable an atmosphere of shared problem-solving that ultimately benefits both the people and wildlife living there.

Thank you for considering these comments. We submit them and associated information in the spirit of continued collaboration with the Forest Service and associated stakeholders of Thunder Basin, especially regarding ways we can contribute to a fuller implementation of the Management Plan, including the Black-tailed Prairie Dog Conservation Assessment and Strategy. We look forward to continuing to work with you on these complex management issues. If you have questions, please do not hesitate to contact us to discuss them.

XII. Literature Cited

See attachments in subsequent pages.

Literature cited in Section III

USFS, MBRNF & TBNG. 2017. U.S. Forest Service Announces One-year Suspension of black-tailed prairie dog shooting restrictions on Thunder Basin National Grassland. Press Release. March 3.

USFS, TBNG (United States Forest Service, Thunder Basin National Grassland). 2014. Completed prairie dog management on Thunder Basin National Grassland. Unpublished report, 12 p.

Literature cited in Section IV

USFWS (United States Fish and Wildlife Service). 2013. Recovery Plan for the Black-footed Ferret (*Mustela nigripes*), Second Revision. United States Fish and Wildlife Service, Region 6.

Literature cited in Section V

Bangert, R. K., and C. N. Slobodchikoff. Conservation of prairie dog ecosystem engineering may support arthropod beta and gamma diversity. *Journal of Arid Environments* 67, no. 1 (2006): 100-115.

Coppock, D. Layne, and James K. Detling. "Alteration of bison and black-tailed prairie dog grazing interaction by prescribed burning." *The Journal of Wildlife Management* (1986): 452-455.

Fuhlendorf, S.D., B.W. Allred and R.G. Hamilton. 2010. Bison as keystone herbivores on the Great Plains. Can cattle serve as proxy for evolutionary grazing patterns? American Bison Society Working Paper No. 4, November 2010.

Hanson, David A., Hugh B. Britten, Marco Restani, and Leigh R. Washburn. "High prevalence of Yersinia pestis in black-tailed prairie dog colonies during an apparent enzootic phase of sylvatic plague." *Conservation Genetics* 8, no. 4 (2007): 789-795.

Knopf, F. L. 1996. Prairie legacies—Birds. Pages 135–148 in F.B. Samson, and F.L. Knopf (eds), Prairie Conservation: Preserving North America's Most Endangered Ecosystem. Washington, D.C.: Island Press.

Kohl, M.T., Krausman, P.R., Kyran K., Williams, D.M. 2013. Bison versus cattle: are they ecologically synonymous? Rangeland Ecology and Management. Society for Range Management. 66(6): 721-731.

Kotliar, Natasha B., Bruce W. Baker, April D. Whicker, and Glenn Plumb. "A critical review of assumptions about the prairie dog as a keystone species." *Environmental management* 24, no. 2 (1999): 177-192.

Miller, Brian, Gerardo Ceballos, and Richard Reading. "The prairie dog and biotic diversity." *Conservation biology* 8, no. 3 (1994): 677-681.

Mulhern, D.W., and C.J. Knowles. Black-tailed prairie dog status and future conservation planning. 1996. Conserving Biodiversity on Native Rangelands: Symposium Proceedings, August 17,1995. D.W. Uresk, G.L. Schenbeck, and J.T. O'Rourke (technical coordinators). General Technical Report RM-GTR-298. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 38 p.

Santos-Barrera, Georgina, Jesús Pacheco, and Gerardo Ceballos. "Amphibians and reptiles associated with the prairie dog grasslands ecosystem and surrounding areas at the Janos Casas Grandes complex, northwestern Chihuahua, Mexico." *Acta zoológica mexicana* 24, no. 3 (2008): 125-136.

Schultz, C.A., Sisk, T.D., Noon, B.R., and M.A. Nie. 2012. Wildlife conservation planning under the United States Forest Service's 2012 planning rule. The Journal of Wildlife Management. 77: 428-444.

Truett, J. C., M. Phillips, K. Kunkel, and R. Miller. 2001. Managing bison to restore biodiversity. Great Plains Research (11): 123-144.

Uresk, D.W., G.L. Schenbeck, J.T. O'Rourke (technical coordinators). 1996. Conserving Biodiversity on Native Rangelands: Symposium Proceedings, August 17, 1995. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. General Technical Report RM-GTR-298. 38 p.

USFS (United States Forest Service). 2001. Biological Assessment and Evaluation, Appendix H, Final Environmental Impact Statement for the Northern Great Plains Management Plans Revision.

USFWS (United States Fish and Wildlife Service). 2013. Recovery Plan for the Black-footed Ferret (*Mustela nigripes*), Second Revision. United States Fish and Wildlife Service, Region 6.

Wang, H., S.D. Schubert, R.D. Koster, and Y. Change. 2019. Attribution of the 2017 Northern High Plains drought. Explaining Extreme Events of 2017 from a Climate Perspective. S.C. Herring, N. Christidis, A. Hoell, M.P. Hoerling, and P.A. Stott (eds). Bulletin of the American Meteorological Society. 100(1): S1-S117.

WGFD (Wyoming Game and Fish Department) and WBFFWG (Wyoming Black-footed Ferret Working Group). 2018. Wyoming Black-footed Ferret Management Plan. November 14.

Literature cited in Section VIII

Buseck, R.S., D.A. Keinath, and E. Everett. 2005. Species Assessment for Black-tailed Prairie Dog (*Cynomys ludovicianus*) in Wyoming. Prepared for United States Department of the Interior, Bureau of Land Management, Wyoming State Office. February.

EPA (Environmental Protection Agency). 2004. Potential Risks of Nine Rodenticides to Birds and Nontarget Mammals: A Comparative Approach. Office of Pesticides Programs, Environmental Fate and Effects Division, Environmental Protection Agency. July.

Gaines, E. 1996. Creating a reserve within the Thunder Basin National Grasslands. Thesis. University of Montana.

Hillman, C.N. 1968. Field observations of black-footed ferrets in South Dakota. In Thirty-third North American Wildlife Conference. Pp. 433-443.

Henderson, F.R., P.F. Springer, and R. Adrian. 1969 (revised 1974). The black-footed ferret in South Dakota. South Dakota Dept. of Game, Fish and Parks Technical Bulletin No. 4. 37 pp.

Lindner, R.L., R.B. Dahlgren, and C.N. Hillman. 1972. Black-footed ferret—prairie dog interrelationships. Pages 22-37 in Symposium on Rare and Endangered Wildlife of Southwestern United States, New Mexico Department of Game and Fish, Sante Fe.

Lockhart, J.M., E.T. Thorne, and D.R. Gober. 2006. A Historical Perspective on Recovery of the Black-footed Ferret and the Biological and Political Challenges Affecting Its Future. Recovery of the black-footed ferret—progress and continuing challenges: U.S. Geological Survey Scientific Investigations Report 2005–5293. J.E. Roelle, B.J. Miller, J.L. Godbey and D.E. Biggins (eds). 288 p.

Luce, R.J. 2006. Areas where habitat characteristics could be evaluated to identify potential black-footed ferret reintroduction sites and develop conservation partnerships. Recovery of the black-footed ferret—progress and continuing challenges: U.S. Geological Survey Scientific Investigations Report 2005–5293. J.E. Roelle, B.J. Miller, J.L. Godbey and D.E. Biggins (eds). 288 p.

Luce, R.J. 2008. Potential black-footed ferret reintroduction sites, 2008. Report to the U.S. Fish and Wildlife Service, Pierre, SD. 51pp.

Matthews, M. 2001. Varmint hunters sidelined in Wyoming. High Country News. July 2.

Pauli, J.N., and S.W. Buskirk. 2007. Recreational shooting of prairie dogs: a portal for lead entering wildlife food chains. Journal of Wildlife Management. 71(1): 103-108.

Rattner, B.A., K.E. Horak, R.S. Lazarus, S.L. Schultz, S. Knowles, B.G. Abbo, and S.F. Volker. 2015. Toxicity reference values for chlorophacinone and their application for assessing anticoagulant rodenticide risk to raptors. Ecotoxicology. 24(4): 720-734.

Select Federal Natural Resource Management Committee of the Wyoming Legislature. 2018. Letter from Senator Michael Von Flatern and Representative Tyler Lindholm to Mr. Scott Talbott (Director, WGFD), Ms. Noreen Walsh (Regional Supervisor, Mountain-Prairie Region, USFWS), and Mr. Brian Ferebee (Regional Forester, Rocky Mountain Region, Forest Service), re: Black-footed Ferret/Reintroduction in the Thunder Basin National Grassland. December 3.

Stephens, R.M., A.S. Johnson, R. Plumb, K.K. Dickerson, and M.C. Mckinstry. 2005. Secondary lead poisoning in golden eagle and ferruginous hawk chicks consuming shot black-tailed prairie dogs, Thunder Basin National Grassland, Wyoming. US Fish & Wildlife Publications. 230.

USFS (United States Forest Service). 2017. Letter to the Wyoming County Commissioners Association from Mr. Brian Ferebee, Regional Forester of the Rocky Mountain Region. May 19.

USFS, MBNF (United States Forest Service, Medicine Bow National Forest). 1998. Medicine Bow National Forest Land and Resource Management Plan Annual Monitoring and Evaluation Report Fiscal Year 1998, Land and Resource Management Plan.

USFS, MBNF (United States Forest Service, Medicine Bow National Forest). 1985. Biological Assessment for the Medicine Bow National Forest and Thunder Basin National Grassland Draft Land and Resource Management Plan. January 19.

USFS, MBNF & TBNG (United States Forest Service, Medicine Bow National Forest and Thunder Basin National Grassland). 1985. Final Environmental Impact Statement for the Medicine Bow National Forest and Thunder Basin National Grassland Land and Resource Management Plan.

USFS, MBRNF & TBNG (United States Forest Service, Medicine Bow-Routt National Forests and Thunder Basin National Grassland), United States Fish and Wildlife Service, and Wyoming Game and Fish Department. 2017. Interagency Statement. December 4.

USFS, TBNG (United States Forest Service, Thunder Basin National Grassland). 2009. Record of Decision, Thunder Basin National Grassland Prairie Dog Management Strategy and Land and Resource Management Plan Amendment #3.

USFS, TBNG (United States Forest Service, Thunder Basin National Grassland). 2014. Completed Prairie Dog Management on Thunder Basin National Grassland.

USFWS (United States Fish and Wildlife Service). 1985. Biological Opinion, Consultation on the effects of the Medicine Bow National Forest Plan. March 22.

USFWS (U.S. Fish and Wildlife Service). 2007. National Bald Eagle Management Guidelines.

USFWS (United States Fish and Wildlife Service). 2013. Black-footed Ferret Recovery Plan, Second Revision. November.

Literature cited in Section X

Fuhlendorf, S.D., B.W. Allred and R.G. Hamilton. 2010. Bison as keystone herbivores on the Great Plains. Can cattle serve as proxy for evolutionary grazing patterns? American Bison Society Working Paper No. 4, November 2010.

Knopf, F. L. 1996. Prairie legacies—Birds. Pages 135–148 in F.B. Samson, and F.L. Knopf (eds), Prairie Conservation: Preserving North America's Most Endangered Ecosystem. Washington, D.C.: Island Press.

Kohl, M.T., Krausman, P.R., Kyran K., Williams, D.M. 2013. Bison versus cattle: are they ecologically synonymous? Rangeland Ecology and Management. Society for Range Management. 66(6):721-731.

Sierra-Corona R., Davidson A., Fredrickson EL., Luna-Soria H., Suzan-Azpiri H., Ponce-Guevara E, et al. (2015) Black-Tailed Prairie Dogs, Cattle, and the Conservation of North America's Arid Grasslands. PLoS ONE 10(3): e0118602. https://doi.org/10.1371/journal.pone.0118602

USFS (United States Forest Service). 2001. Biological Assessment and Evaluation, Appendix H, Final Environmental Impact Statement for the Northern Great Plains Management Plans Revision.

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Conservation of prairie dog ecosystem engineering may support arthropod beta and gamma diversity

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Abstract

Ecosystem engineering by animals can create new habitats and increase the heterogeneity of the habitat mosaic that in turn can increase plant and animal diversity. Prairie dogs in North America alter both the above- and below-ground structure of the landscape and create novel habitats in grassland ecosystems. The ground-dwelling arthropod community associated with Gunnison's prairie dog modified habitats is compositionally different from that found in the surrounding grassland. Individual arthropod families and species have different distributions in both active prairie dog towns and inactive towns, compared to unmodified grasslands. These different responses to ecosystem engineering increase beta (between-habitat) and gamma (regional) diversity. This study suggests that simple measures of alpha diversity (species richness) may not adequately quantify overall diversity and that measures of beta diversity may be necessary to assess the role of prairie dogs as keystone engineers. Thus, conservation of prairie dogs and the engineering process may have positive effects for numerous species both locally and regionally.

Keywords: Arthropod assemblage; Conservation; High desert grasslands; Ecosystem engineering; Gunnison's prairie dog; Keystone species; Petrified Forest National Park

1. Introduction

A critical issue in ecology is to determine the mechanisms behind the patterns of community assemblages. Once these mechanisms are better understood conservation

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biologists will better be able to prioritize conservation efforts. Two relevant and important concepts in conservation theory are keystone species and ecosystem engineers (Lomolino and Smith, 2003). Keystone species confer inordinate effects relative to their abundance or provide unique services (Power et al., 1996; Kotliar, 2000). Ecosystem engineers modify their habitat and these modifications may have positive or negative effects on other species (Jones et al., 1997). Although the keystone concept can be contentious (Stapp, 1998; Miller et al., 2000), as more studies are published it is clear that ecosystem engineering can be one mechanism that confers keystone status to a species (e.g. Lomolino and Smith, 2003) through the impact that they have on ecosystems (Jones et al., 1994, 1997; Brown, 1995; Kotliar, 2000). These effects can have far-reaching consequences that can affect not only ecological associations, but also the behavior of animals within an ecosystem. For example, we have recently shown that keystone-engineering influences landscape structure, which then in turn affects animal movement behavior (Bangert and Slobodchikoff, 2000, 2004).

A major class of effects comes in the form of mechanical ecosystem engineering where an organism modifies or creates habitat through its activities (e.g. beaver; Wright et al., 2002). For example, the activities of pocket gophers can have ecosystem level effects that influence plant diversity at small scales (Huntly and Inouye, 1988; Martinsen et al., 1990) and influence the distribution of aspen at large scales (Cantor and Whitham, 1989). Other examples include leaf-modifying insects whose structures enhance richness and abundance of inquilines and other arthropods (Martinsen et al., 2000; Lill and Marquis, 2003), and kangaroo rat mounds that influence the distribution of arthropods and vertebrates (Hawkins and Nicoletto, 1992). If the ecosystem engineer is rare, its overall effect may be large relative to its biomass and therefore provides a unique ecological service and can be classified as a keystone species (Power et al., 1996; Kotliar, 2000). Consequently, ecosystem engineering can have important conservation consequences by creating a landscape mosaic that influences the structure of vertebrate communities and increases the richness of avian species of conservation concern (Lomolino and Smith, 2003; Smith and Lomolino, 2004).

Ecosystem engineering has been demonstrated for two species of prairie dogs (Sciuridae: *Cynomys* spp.) in North America (Weltzin et al., 1997a, b; Ceballos et al., 1999; Bangert and Slobodchikoff, 2000), but concerns have been raised about the strength of the evidence supporting prairie dogs as keystones based on species associations (Stapp, 1998). Although the effects prairie dogs have on soils and plants is well understood (Carlson and White, 1987; Whicker and Detling, 1988; Munn, 1993; Weltzin et al., 1997a, b), only recently has evidence for the relationship between prairie dogs and faunal communities been well documented (e.g. Lomolino and Smith, 2003; Smith and Lomolino, 2004). Previously most work has been conducted on the functional relationships between prairie dogs and a few charismatic vertebrates of concern (Knowles et al., 1982; Krueger, 1986; Clark et al., 1989; Oldemeyer et al., 1993; Desmond et al., 1995; Desmond and Savidge, 1996; Kotliar et al., 1999), and these studies have focused on associations with the black-tailed prairie dog, *C. ludovicianus*, in mixed and short grass prairie (but see Davidson et al., 1999). However, there are five species of prairie dogs that occupy a range of grassland habitat types in the western Great Plains and Intermountain West from Canada to Mexico (Goodwin, 1995; Hoogland, 1995, p. 12) potentially resulting in region-wide ecosystem engineering effects with large-scale conservation implications.

In this study, we investigate the relationship between the Gunnison's prairie dog (*C. gunnisoni*) and a grassland arthropod community, for three reasons. First, prairie dogs have significant above- and below-ground ecosystem level impacts (Vogel et al., 1973;

Carlson and White, 1987; Munn, 1993; Ceballos et al., 1999; Bangert and Slobodchikoff, 2000). Second, because arthropods represent over half of worldwide multi-cellular biodiversity (Crawford, 1981, 1991), arthropods are important ecosystem components (Seastedt, 1984; Kremen et al., 1993; Anderson, 1995; Parmelee, 1995), and little work has been done on the relationship between prairie dogs and arthropod communities (e.g. O'Meilia et al., 1982). Third, since prairie dog ecosystem engineering has been shown to have a positive effect on the richness and structure of vertebrate communities of conservation concern (Lomolino and Smith, 2003; Smith and Lomolino, 2004), it is important to quantify the relationship between prairie dog engineering and lower trophic levels. We use a comparative approach to take advantage of a natural experiment (sensu Diamond, 1986), and make the following predictions. Prairie dog habitat modification leads to: (1) differential responses by individual arthropod species to prairie dog-modified habitats; (2) this results in high beta (between habitat) diversity in arthropod community structure between prairie dog towns and unmodified grasslands; (3) high levels of beta diversity result in greater species richness across the landscape (gamma diversity).

2. Materials and methods

2.1. Study site

This work was conducted on the high desert grasslands (1600–1750 m above sea level) at Petrified Forest National Park (PEFO), Arizona, USA, during 1996 and 1997 from 1 June through 30 July. Petrified Forest has an average annual precipitation of 24.4 cm and average high temperatures ranging from 0.8 °C in January to 23.5 °C in July. Precipitation exhibits a single peak in July and August due to the summer monsoon. The vegetation at PEFO is characterized as shrub-steppe dominated by the large shrubs *Atriplex canescens*, *Artemisia filifolia*, and *Ar. Biglovii*, and the smaller *At. jonesii* and *At. confertifolia*. The grasses *Bouteloua gracilis*, *Stipa hymenoides,* and *Sporobolus* spp. are common (Kierstead, 1981).

2.2. The ecosystem engineer

The Gunnison's prairie dog (*Cynomys gunnisoni* Hollister) is a medium sized (675–1350 g) ground squirrel in the family Sciuridae. This species is found on the Colorado Plateau extending across four states in North America: Arizona, Colorado, New Mexico, and Utah (Fitzgerald et al., 1994; Goodwin, 1995). Gunnison's prairie dogs are colonial and social animals (Slobodchikoff, 1984; Hoffmeister, 1986; Fitzgerald et al., 1994), and prairie dog colonies, or towns, are conspicuous features of North American grassland ecosystems. Activities of prairie dogs include alteration of soil chemistry and extensive soil movement (Carlson and White, 1987; Munn, 1993; Ceballos et al., 1999), herbivory (Whicker and Detling, 1988), and granivory (Shalaway and Slobodchikoff, 1988), resulting in significant changes in the fractal dimension of landscape spatial structure and shrub distribution (Bangert and Slobodchikoff, 2000).

2.3. Experimental design

This study took advantage of a natural experiment (Diamond, 1986) where the landscape was manipulated by the Gunnison's prairie dog and 100% of the prairie dogs were extirpated from two of the five prairie dog towns by plague (*Yersina pestis*; Cully, 1989; Fitzgerald, 1993) 15 months prior to the beginning of this study resulting in a BACI-style experiment (B = before, A = after intervention, C = control, and I = Intervention; Stewart-Oaten et al., 1986, 1992). Natural experiments offer an important opportunity for study because it is both difficult and unethical to manipulate animals and landscapes at large scales, and this is particularly relevant to conservation studies (Farnsworth and Rosovsky, 1993; Brown, 1995; Lomolino and Smith, 2003). There were three levels of natural habitat variability in this study: (1) habitats with no modification by prairie dogs representing before and control effects (B and C; grasslands), (2) habitats previously modified by prairie dogs but with no prairie dogs present representing the after intervention effect (A; inactive towns), and (3) habitats with prairie dogs present (active towns) represent the intervention (I) aspects of a BACI-type experimental design.

In 1996 three active prairie dog towns, two inactive prairie dog towns, and five grassland habitats were sampled for ground-dwelling arthropods. One active site and a nearby grassland site were sampled concurrently for five consecutive days, and then an inactive site and another grassland site were sampled concurrently. Additional active, inactive, and grassland sites were alternately sampled in order to reduce temporal pseudoreplication (Hurlbert, 1984) resulting in a total of 2500 trap days. Each grassland site was <1 km from the nearest prairie dog town. In 1997 access to towns was restricted because of archeological concerns, so increased effort was concentrated at one active town, one inactive town, and a grassland site located approximately 6 km in-between the two prairie dog towns. All three sites were sampled concurrently for 19 days resulting in 2850 trap days. During both years 50 pitfall traps were distributed randomly over 1 ha at each site. Arthropods were identified to family, and we feel that this provides good resolution and a conservative approach for this study. For example, at the family level most species can be categorized by trophic status, with the exception of the ants (Formicidae).

Traps were 12 oz. Solo® plastic cups nested in 16 oz. cups set flush with the ground surface. Each trap had an elevated plywood lid for shade (900 cm^2) to protect animals from the sun. Each morning, traps were checked, arthropod identification was determined to family level and the arthropods were counted and then released in a random direction ≈ 3 m from the trap. Large mobile animals were marked with a unique number to avoid recounting. Animals not identified to family were collected for later identification and "Day" was the sample unit used in the composition analysis. Since all traps in 1997 were sampled concurrently, we checked for temporal autocorrelation by examining residuals and the Durbin–Watson test indicating that there was no autocorrelation between days and therefore days were regarded as independent. Every site was subjected to the same sampling regime and the weather was consistent throughout the sampling period from 1 June through 30 July within each year. In 1997 the distance from each trap was quantified to the nearest burrow to assess the arthropod relationship with burrows.

2.4. *Differential effects of above-ground engineering*

2.4.1. *Unique taxa*

Ecosystem engineering hypotheses predict that some species will be positively affected and some negatively affected by mechanical engineering and subsequent habitat alteration

(Jones et al., 1997). First, the number of unique taxa associated with prairie dog towns was quantified. Prairie dog towns were nested within the larger grassland landscape matrix of $\approx$37,851 ha (we estimated that prairie dog towns comprise $<$2% of the landscape area at PEFO). Therefore the null expectation was that the faunas associated with prairie dog towns would also be nested within the overall grassland arthropod family pool. To address this, the proportion of unique families contributed by individual prairie dog towns was assessed with single sample *t*-tests. Individual towns were compared to grasslands at three different scales: (1) versus the nearest grassland site of the same size, (2) versus all grassland sites pooled within the year that the prairie dog site was sampled, and (3) versus all grassland sites pooled across years. This resulted in a test that was increasingly biased in favor of the grassland family pool as grassland scale increased. For this analysis active and inactive towns were considered as the same treatment, resulting in seven replicate prairie dog towns. Under the null hypothesis that the prairie dog arthropod community is a perfectly nested subset of the larger regional grassland family pool, the proportion of unique families found on prairie dog habitats should be zero.

2.4.2. Indicator taxa

The occurrence of indicator taxa for each habitat was quantified with the software program INDVAL (Dufrêne and Legendre, 1997). Indicator taxa are determined by the distribution of individuals within each taxon across samples and treatments. The indicator value, *I*, indicates the percent predictability of sampling a particular taxon in a particular habitat type with *p*-values determined by Monte Carlo methods. For example, if ants were found in all samples within only one habitat type they would have an indicator value of $I = 100.00$ for that habitat.

In order to assess the effects of above-ground engineering on community structure, the 1996 arthropod community was quantified at each site ($n = 10$) with nonmetric multidimensional scaling (NMDS; Minchin, 1987, 1999) and the community one-dimensional solution ordination scores were regressed against the fractal dimension of each site (Anderson, 2001). Landscape fractal dimension was used as a measure of ecosystem engineering, where sites with large fractal dimensions were associated with heavily modified prairie dog habitats (Bangert and Slobodchikoff, 2000).

2.5. Relationship with below-ground structures

To assess the effects of below ground engineering, i.e. burrows, in 1997 we modeled the distribution of two abundant beetle species in the family Tenebrionidae and crickets in the family Gryllacrididae, and their relationship to prairie dog burrow proximity with loglinear regression (Agresti, 1996). In 1998, traps were placed at 1 and 5 m from burrow entrances. Pairs of traps were placed at random at a grassland site and randomly designated as the "1 m" or "5 m" traps. This was done because adding a burrow treatment to a grassland site was not permitted because of archaeological concerns in the Park. Additionally, at the community level Mantel tests were used to assess the relationship between abundance and community structure with distance from burrows. If burrows do not influence these animals, the null hypothesis predicts that traps at all distances from burrows will trap similar numbers of animals and have similar communities.

2.6. Community structure

In this study we concentrate on beta diversity (community structure between habitats) because alpha diversities (e.g. species richness between habitats) may not be different but community structure can be very different (Bangert et al., 2005; Wimp et al., 2005). Beta diversity was assessed as dissimilarity in community structure between habitats, and was quantified with the powerful ordination technique, Canonical Analysis of Principal coordinates (CAP; Anderson and Willis, 2003) and the Bray–Curtis similarity coefficient (Bray and Curtis, 1957; Kruskal, 1964; Faith et al., 1987; Minchin, 1987; Clarke, 1993; Legendre and Legendre, 1998; Dungey et al., 2000). Additionally, pairwise comparisons were conducted between all treatments and randomization tests were used to determine *p*-values. These *p*-values are reported without any correction for multiple tests so that readers can make their own determination as to the strength of the treatment effects. CAP is appropriate for these data because the procedure corrects for the effect of taxa that are correlated across treatments. Finally, we use accumulation curves to assess the contribution of the prairie dog treatments to gamma, i.e. regional diversity.

3. Results

3.1. Differential effects of above-ground engineering

3.1.1. Unique taxa

Unique families were found in both prairie dog and grassland habitats. Prairie dog and grassland habitats contributed 6 and 10 unique families, respectively. Even though there were not consistent differences in richness between individual prairie dog towns and the nearest grassland site, at all scales prairie dog towns contributed more unique taxa than expected by chance if they were simple subsets of the grassland family pool (vs. nearest grassland: $t = 6.78$, df = 6; $p = 0.0005$; vs. grasslands pooled within year: $t = 4.15$, df = 6; $p = 0.003$; vs. all grasslands pooled across years: $t = 1.91$, df = 6; $p = 0.053$; Fig. 1a). For example, the 1997 ordered accumulation curve shows that prairie dog-modified habitats contribute families beyond the families found on grassland habitats even though there were no differences in richness among treatments (Fig. 1b; the 1996 accumulation curve was similar to the 1997 curve). These data suggest that prairie dog activities significantly affect this ground-dwelling arthropod community at different scales, and the quantification of beta diversity is as informative as alpha diversity (Su et al., 2004).

3.1.2. Indicator taxa

There were several families that were significant indicators for each of the three habitat types in this study. The response by different families to different habitats was what might be expected. For example, the insect herbivore family, Cicadellidae, was almost 10 times more abundant on grasslands relative to prairie dog habitats ($z = 4.50$, $p < 0.0001$), while the Scarabaeidae was 13 times more abundant on active prairie dog towns where scats were abundant ($z = 3.09$, $p = 0.001$). Indicator value analysis suggests that over the course of this study, Cicadellidae were the only significant indicators of grasslands. Pholcidae, Mutillidae, Curculionidae, Cerambicidae, and Isopoda were significant indicators of inactive towns, and Salticidae, Gelichiidae, and Gryllidae were significant indicators of

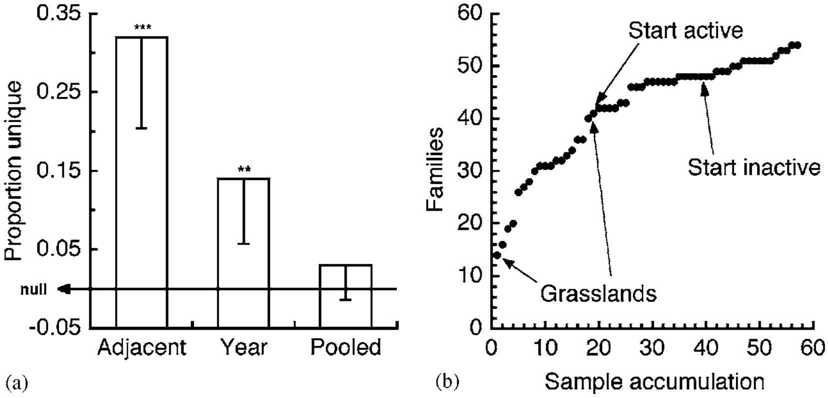

Fig. 1. (a) Mean proportion of unique families contributed to the grassland ecosystem by seven prairie dog towns at different scales. One-sample *t*-tests of these proportions on individual prairie dog towns versus the null hypothesis that prairie dog habitats are subsets of the greater grassland ecosystem with the proportion of unique families equal to zero. "Adjacent" is individual towns versus the nearest grassland site, "Year" is individual towns versus all grassland communities pooled for that year, and "Overall" is individual towns versus all grassland communities pooled across years, resulting in an increased bias, in favor of the null hypothesis, as grassland scale increases. Horizontal line represents the null hypothesis. Error bars represent the lower 95% confidence interval, two asterisks indicates significance at $p<0.01$, and three asrterisks indicate $p<0.001$. (b) 1997 ordered accumulation curve (grasslands-active-inactive) of family richness where all three habitats had similar numbers of families, but active and inactive towns add unique families beyond what the grasslands contribute. The 1996 accumulation curve is similar to the 1997 accumulation curve.

Table 1
Arthropod families that were significant indicators of habitat types on the grasslands at Petrified Forest National Park, AZ, USA

	Active		Inactive		Grasslands		Functional group
Family	IndVal	*t*-value	IndVal	*t*-value	IndVal	*t*-value	
Salticidae	19.2	3.24					Predator
Gryllidae	16.6	4.18					Herbivore
Gelechiidae	18.1	4.86					Herbivore
Pholcidae			43.9	4.43			Predator
Isopoda			21.4	4.20			Omnivore
Cerambicidae			24.7	5.53			Herbivore
Curculionidae			26.5	2.90			Herbivore
Mutillidae			43.2	4.84			Parasitoid
Cicadellidae					32.0	5.58	Herbivore

active towns (Table 1). This analysis supports the hypothesis that different taxa respond differently to prairie dog engineering and this results in high arthropod beta diversity.

3.2. Relationship with below-ground structures

There was a relationship between below ground engineering (burrows) and three conspicuous taxa. The beetle *Eleodes extricata* had greater numbers on the inactive than

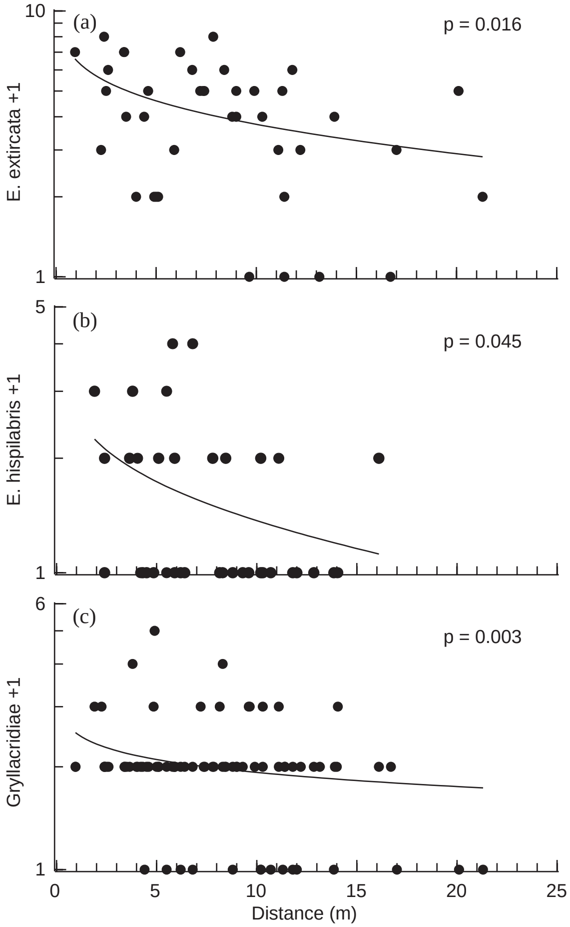

Fig. 2. Beetle and cricket correlations with prairie dog burrows modeled with loglinear regression. *E. extricata* was trapped more often closer to burrows on an inactive prairie dog town (a). *E. hispilabris* (b) and camel crickets (c) were trapped more often closer to burrows on both active and inactive towns.

active town (df = 1, $\chi^2 = 36.6$, $p < 0.0001$) and was trapped more often in close proximity to inactive prairie dog burrows (log beetle = 1.673–0.046 × distance, $p = 0.01$, Fig. 2a). *E. hispilabris* had equal numbers between both prairie dog habitats and was trapped closer to all burrows types (log beetle = 0.492–0.023 × distance, $p = 0.045$, Fig. 2b). Gryllacridid crickets were also trapped more often closer to all burrow types (log cricket = 0.86–0.27 × distance, $p = 0.003$, Fig. 2c). In 1998 trapping frequencies for these three taxa were evaluated at 1 and 5 m from burrow entrances, and in pairs of traps on a grassland site. There were no crickets trapped on the grassland and 233% more crickets trapped in the 1 m traps than in the 5 m traps ($\chi^2 = 29.6$; $p = 0.0001$; df = 2). Likewise, there was only one beetle trapped on the grassland site and 135% more beetles trapped at 1 m than at 5 m from burrow entrances ($\chi^2 = 26.3$; $p = 0.0001$; df = 2). These data suggest that burrows are important to these animals.

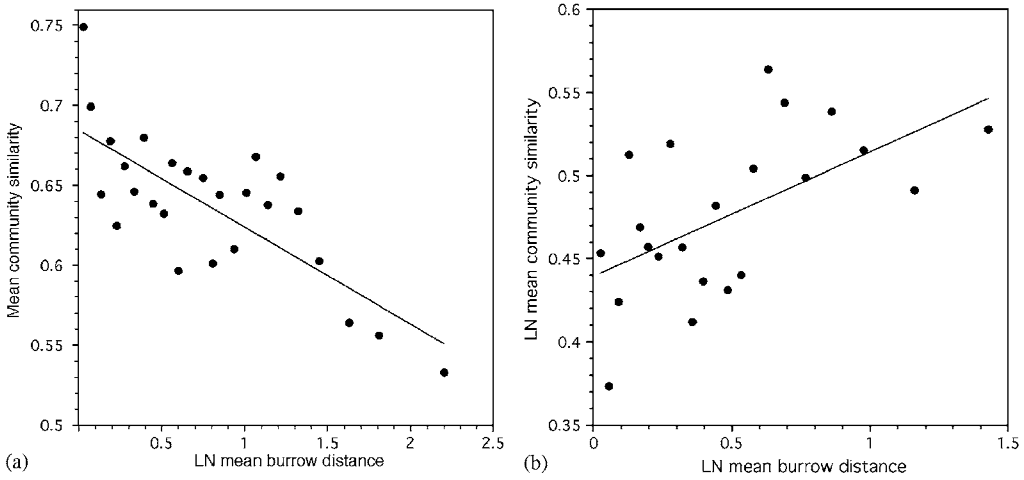

Fig. 3. Arthropod communities are more similar closer to burrows, on average, at the inactive prairie dog town (a), but show the opposite response at the active town where communities are more similar at greater distances from burrows (b). Community similarity is represented by the Bray–Curtis similarity coefficient and similarity in burrow distance is represented by Euclidean distance, where small distances represent communities that are more similar.

Community structure was similar at similar distances from burrows on the inactive town (Mantel $r = -0.3146$, Mantel $t = -3.44$, $p = 0.0003$, $n = 26$; Fig. 3a), and the pattern was opposite on the active town (Mantel $r = 0.1897$, Mantel $t = 1.91$, $p = 0.03$, $n = 22$; Fig. 3b). In other words, community structure changes with proximity to burrows differently between these two habitats, which suggests that there may be differences in burrow environments between active and inactive towns resulting in a habitat mosaic that increases beta diversity.

The above-ground engineering component showed that 22 families had significantly greater relative abundances among the three different habitats, but these were equally distributed (active = 8; inactive = 7, grass = 7), suggesting that alpha diversity alone is not sufficient to characterize differences between treatments. This analysis also supports the hypothesis that ecosystem engineering affects taxa differently. Overall, 68% of these families showed a positive response to prairie dog engineered landscapes, inactive and active combined. At the community level habitats with similar landscape structures, measured by fractal dimension, had similar arthropod community structures ($r^2 = 0.4849$, $p = 0.025$, $F_{1,8} = 7.53$; Fig. 4).

3.3. Community structure

Over 2 years of this study, 2315 arthropod individuals were distributed over 68 families in 5350 trap days. There were differences in community structure by habitat and a Canonical Analysis of Principal coordinates (CAP; Anderson and Willis, 2003) indicated that the arthropod community in each habitat was unique (1996: all pairwise $p \leqslant 0.002$, Fig. 5a; 1997: all pairwise $p \leqslant 0.0002$, Fig. 5b).

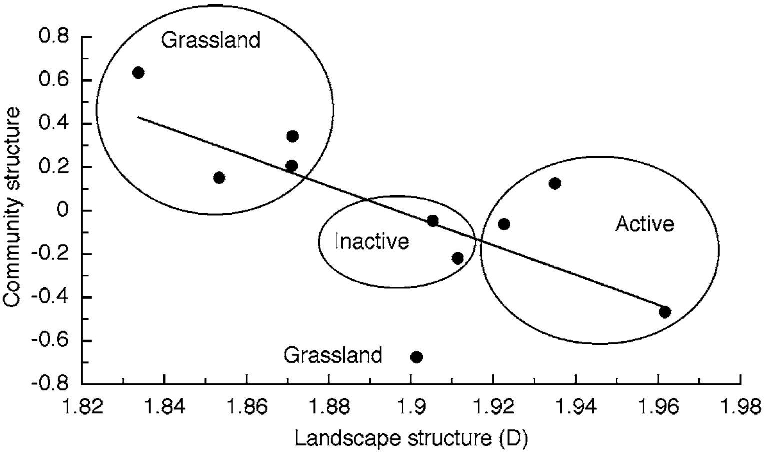

Fig. 4. Arthropod community structure at each site (1996) changes with an increase in prairie dog engineering. The mean landscape fractal dimension of each site is a measure of engineering, where large fractal dimension indicates more intensive prairie dog activity. Arthropod community structure is based on the one-dimensional NMDS ordination scores, which place a multivariate community into one-dimensional Euclidean space with no a priori expectation on the slope of the relationship, but rather, community composition changes with engineering. Site treatments are encompassed by ellipses.

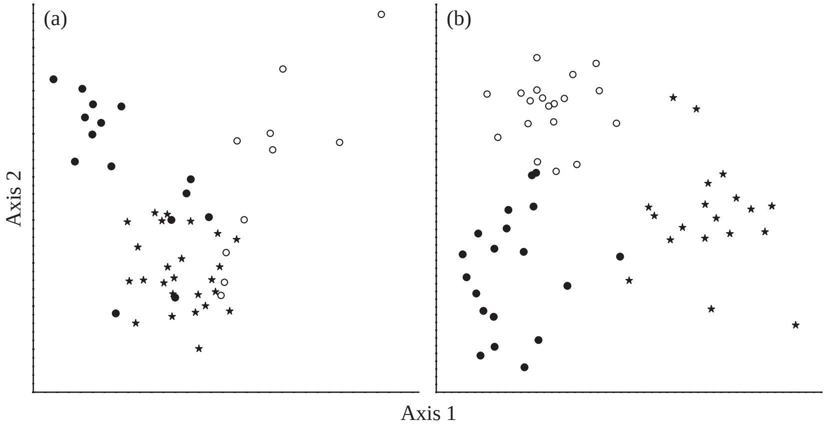

Fig. 5. Canonical analysis of principal coordinates (CAP) of community composition where axes are unit-less and only serve to place points in ordination space; points close together are more similar than points that are more distant. (a) Arthropod community structure at 10 sites × 5 days for 1996, and (b) for the 3 sites × 19 days in 1997. In both years the communities are significantly dissimilar across the three treatments. Active = ●; Inactive = ○; Grasslands = ★.

4. Discussion

This is the first community-level study that examined the effects of ecosystem engineering by the Gunnison’s prairie dog on arthropods, comparing active and inactive prairie dog towns with unmodified grasslands. In this study both above- and below-ground prairie dog engineering was significantly correlated with several arthropod species, and with community structures between each prairie dog habitat and the grassland matrix. The high beta diversity associated with the presence of prairie dogs resulted in an increase in gamma diversity within Petrified Forest National Park. For example, family richness was the same for the three habitats and yet an analysis of community structure indicated that there were distinct communities associated with the three habitat types in this study. High beta diversity is likely due to individual responses by different taxa to prairie dog engineering as predicted by one ecosystem engineering hypothesis (Jones et al., 1997). For example, prairie dogs may be contributing detritus (see Hawkins and Nicoletto 1992 with reference to kangaroo rat contribution of detritus), thus detritivores (e.g. Scarabaeidae rolling scats, pers. obs.) may become more abundant in prairie dog modified habitats, whereas herbivory by prairie dogs may exclude insect herbivores such as the Cicadellidae in the active towns. We found that there were a significant proportion of unique families associated with both types of prairie dog habitats over a large range of scales. Thus, without prairie dogs there would be no beta diversity component and gamma diversity would likely be 33% lower (Fig. 1b). On the high desert grasslands of Petrified Forest, prairie dog engineering appears to create a habitat mosaic that significantly influences the arthropod community at several scales. This suggests that prairie dogs play a unique role in this desert grassland ecosystem and therefore, they may be a keystone to this faunal community (e.g. Kotliar, 2000). We expect that if a finer resolution of taxa were used, e.g. the species level, these patterns would become stronger.

We used the fractal dimension of landscape structure as a measure of above-ground ecosystem engineering (Bangert and Slobodchikoff, 2000) and found that sites with similar levels of ecosystem engineering also had similar community structures. An alternative hypothesis is that the presence of prairie dogs on the active town inhibits arthropod activity. We do not favor this hypothesis because insects are not a significant component of prairie dog diets (Fagerstone et al., 1981; Shalaway and Slobodchikoff, 1988). Another alternative hypothesis is that arthropods are responding to changes in floristic structure due to prairie dog activities; however, we did not test this hypothesis, although, changes in floristic structure have been shown to result from prairie dog engineering activities (Archer et al., 1987; Whicker and Detling, 1988, 1993; Weltzin et al., 1997a, b).

Because there were different responses to burrows among arthropod species and communities between the active and inactive towns, this suggests that there may be differences in burrow environments between these towns (see Hawkins and Nicoletto). One hypothesis is that burrows on the active town are maintained in an open condition facilitating burrow self-ventilation resulting in lower levels of relative humidity (Vogel et al., 1973), potentially affecting arthropod osmoregulation (e.g. Riddle et al., 1976; Slobodchikoff, 1983; Whicker and Tracy, 1987; Parmenter et al., 1989), whereas the burrow entrances on inactive towns become closed with time (pers. obs.) thus inhibiting the ventilation process, resulting in a more equable environment (e.g. Schmidt-Nielson and Schmidt-Nielson, 1950).

The above- and below-ground results support the hypothesis that ecosystem engineering by the Gunnison's prairie dog provides a unique ecological service (Kotliar, 2000) that may enhance arthropod diversity. These results do not suggest that we can eliminate prairie dogs in order to create inactive town habitats, but rather support the hypothesis that prairie dog engineering results in a mosaic of habitat conditions, i.e. landscape heterogeneity, that increase beta and gamma diversity (e.g. active habitats also contain unique species). All species of prairie dogs are suffering dramatic population declines due to human activities, persecution, and the exotic epizootic plague, *Y. pestis* (Miller and Cully, 2001). Thus, prairie dogs require conservation attention and consideration as threatened species, as well as their importance in creating habitat mosaics that are important to many invertebrate and vertebrate species (Lomolino and Smith, 2003).

Prairie dog towns are important to many vertebrate species of concern (e.g. black-footed ferrets, bald eagles, ferruginous hawks, and burrowing owls) and influence mammal, herptile, and avian community structure (Lomolino and Smith, 2003; Smith and Lomolino, 2004). This is the first community level study to demonstrate that prairie dog habitats are also important to invertebrates. This is of conservation concern because the diversity of animals at the base of the food web has the potential for a bottom-up contribution to ecosystem function, and the diversity of taxa at higher levels may be mediated by prairie dog engineering. For example, other studies have found higher abundance of small mammals (O'Meilia et al., 1982; Agnew et al., 1986, 1988), significant differences in mammal community structure, and higher diversity of vertebrate species of conservation concern (Lomolino and Smith, 2003; Smith and Lomolino, 2004) on black-tailed prairie dog towns compared to adjacent grasslands. Most of the species in these studies incorporate arthropods in their diet and this provides the testable hypothesis that diversity at lower trophic levels, i.e. invertebrates, may positively affect diversity at higher trophic levels, i.e. vertebrates, on prairie dog towns. One mechanism for greater vertebrate diversity may be due to high arthropod beta diversity, resulting in a more heterogeneous feeding niche space for vertebrate insectivores.

The prairie dogs' influence on soils and plants (Carlson and White, 1987; Whicker and Detling, 1988, 1993; Munn, 1993) should be sufficient to classify prairie dogs as keystone species. This study is consistent with the hypothesis that prairie dogs may be keystone species to animal communities as a result of their engineering activities (Ceballos et al., 1999; Kotliar et al., 1999; Kotliar, 2000; Miller et al., 2000). As in the grasslands of the Great Plains, the continued loss of prairie dog habitat and the homogenization of this high desert grassland will result in the decline of arthropod diversity, and potentially vertebrate diversity, similar to that described by Lomolino and Smith (2003). This adds support to the more holistic approach of habitat conservation as a more efficient conservation strategy (e.g. Bangert et al., 2005) through the protection of these ecosystem engineers (e.g. Simberloff, 1998) and their extended effects (Smith and Lomolino, 2004), rather than a continuation of the practice of conservation triage where numerous species become threatened due to the loss of the habitat mosaic created and maintained by this class of organisms.

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References

Agnew, W., Uresk, D.W., Hansen, R.M., 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. Journal of Range Management 39, 135–139.

Agnew, W., Uresk, D.W., Hansen, R.M., 1988. Arthropod Consumption by Small Mammals on Prairie Dog Colonies and Adjacent Ungrazed Mixed Grass Prairie in Western South Dakota. Habitat use and Management of Small Mammals and Amphibians. USDA Forest Service, Washington, DC.

Agresti, A., 1996. An Introduction to Categorical Data Analysis. Wiley, New York.

Anderson, J.M., 1995. Soil organisms as engineers: microsite modulation of macroscale processes. In: Jones, C.G., Lawton, J.H. (Eds.), Linking Species and Ecosystems. Chapman & Hall, New York, pp. 94–116.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Australian Journal of Ecology 26, 32–46.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525.

Archer, S., Garrett, M.G., Detling, J.K., 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetation 72, 159–166.

Bangert, R.K., Slobodchikoff, C.N., 2000. The Gunnison's prairie dog structures a high desert grassland landscape as a keystone engineer. Journal of Arid Environments 46, 357–369.

Bangert, R.K., Slobodchikoff, C.N., 2004. Prairie dog engineering indirectly affects beetle movement behavior. Journal of Arid Environments 56, 83–94.

Bangert, R.K., Turek, R.J., Martinsen, G.D., Wimp, G.M., Bailey, J.K., Whitham, T.G., 2005. Benefits of conservation of plant genetic diversity on arthropod diversity. Conservation Biology 19, 379–390.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27, 325–349.

Brown, J.H., 1995. Organisms as engineers: a useful framework for studying effects on ecosystems? Trends in Ecology and Evolution 10, 51–52.

Cantor, L.F., Whitham, T.G., 1989. Importance of belowground herbivory: pocket gophers may limit aspen to rock outcrop refugia. Ecology 70, 962–970.

Carlson, D.C., White, E.M., 1987. Effects of prairie dogs on mound soils. Journal of the Soil Science Society of America 51, 389–393.

Ceballos, G., Pacheco, J., List, R., 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Journal of Arid Environments 41, 161–172.

Clark, T.W., Hinckley, D., Rich, T. (Eds.), 1989. The prairie dog ecosystem: managing for biological diversity. Wildlife Technical Bulletin 2, Montana Bureau of Land Management, Billings.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117–143.

Crawford, C.S., 1981. The Biology of Desert Invertebrates. Springer, Berlin.

Crawford, C.S., 1991. The community ecology of macroarthropod detritivores. In: Polis, G.A. (Ed.), The Ecology of Desert Communities. University of Arizona Press, Tucson, pp. 89–112.

Cully Jr., J.F., 1989. Plague in prairie dog ecosystems: importance for black-footed ferret management. In: Clark, T.W., Hinckley, D., Rich, T. (Eds.), The Prairie Dog Ecosystem: Managing for Biological Diversity. Wildlife Technical Report 2. Montana Bureau of Land Management, Billings, pp. 47–55.

Davidson, A.D., Parmenter, R.R., Gosz, J.R., 1999. Responses of small mammals and vegetation to a reintroduction of Gunnison's prairie dogs. Journal of Mammalogy 80, 1311–1324.

Desmond, M.J., Savidge, J.A., 1996. Factors influencing burrowing owl nest densities and numbers in western Nebraska. American Midland Naturalist 136, 143–148.

Desmond, M.J., Savidge, J.A., Siebert, T.F., 1995. Spatial patterns of burrowing owl (*Speotyto cunicularia*) nests within black-tailed prairie dog (*Cynomys ludovicianus*) towns. Canadian Journal of Zoology 73, 1375–1379.

Diamond, J., 1986. Overview: laboratory experiments, field experiments, and natural experiments. In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper and Row, New York, pp. 3–22.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.

Dungey, H.S., Potts, B.M., Whitham, T.G., Li, H.-F., 2000. Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. Evolution 54, 1938–1946.

Fagerstone, K.A., Tietjen, H.P., Williams, O., 1981. Seasonal variation in the diet of black-tailed prairie dogs. Journal of Mammalogy 62, 820–824.

Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetation 69, 57–68.

Farnsworth, E.J., Rosovsky, J., 1993. The ethics of ecological field experimentation. Conservation Biology 7, 463–472.

Fitzgerald, J.P., 1993. The ecology of plague in Gunnison's prairie dogs and suggestions for the recovery of black-footed ferrets. In: Oldemeyer, J.L., Biggins, D.E., Miller, B.J., Crete, R. (Eds.), Proceedings of the Symposium on the Management of Prairie dog Complexes for the Reintroduction of the Black-Footed Ferret. US Department of the Interior: Fish and Wildlife Service, Washington, DC, pp. 50–58 Biological Report 13.

Fitzgerald, J.P., Meaney, C.A., Armstrong, D.M., 1994. Mammals of Colorado. Denver Museum of Natural History and University Press of Colorado, Denver.

Goodwin, T.H., 1995. Pliocene–Pleistocene biogeographic history of prairie dogs, genus *Cynomys* (Sciuridae). Journal of Mammalogy 76, 100–122.

Hawkins, L.K., Nicoletto, P.F., 1992. Kangaroo rat burrows structure the spatial organization of ground-dwelling animals in a semiarid grassland.

Hoffmeister, D.F., 1986. Mammals of Arizona. University of Arizona Press and the Arizona Game and Fish Department, Tucson.

Hoogland, J.L., 1995. The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal. University of Chicago Press, Chicago.

Huntly, N., Inouye, R., 1988. Pocket gophers in ecosystems: patterns & mechanisms. BioScience 38, 786–793.

Hurlbert, S.H., 1984. Pseudoreplication & the design of ecological field experiments. Ecological Monographs 54, 187–211.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive & negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Kierstead, J.R., 1981. Flora of Petrified Forest National Park, Arizona. MS Thesis, Northern Arizona University, Flagstaff.

Knowles, C.J., Stoner, C.J., Gieb, S.P., 1982. Selective use of black-tailed prairie dog towns by mountain plovers. Condor 84, 71–74.

Kotliar, N.B., 2000. Application of the new keystone-species concept to prairie dogs: how well does it work? Conservation Biology 14, 1715–1721.

Kotliar, N.B., Baker, B.W., Whicker, A.D., Plumb, G., 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24, 177–192.

Kremen, C., Caldwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F., Sanjayan, M.A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7, 796–808.

Krueger, K., 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecology 67, 760–770.

Kruskal, J.B., 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29, 1–27.

Legendre, P., Legendre, L., 1998. Numerical Ecology, second ed. Elsevier, Amsterdam.

Lill, J.T., Marquis, R.J., 2003. Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. Ecology 84, 682–690.

Lomolino, M.V., Smith, G.A., 2003. Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. Biological Conservation 115, 89–100.

Martinsen, G.D., Cushman, J.H., Whitham, T.G., 1990. Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community. Oecologia 83, 132–138.

Martinsen, G.D., Floate, K.D., Waltz, A.M., Wimp, G.M., Whitham, T.G., 2000. Positive interactions between leafrollers and other arthropods enhance biodiversity on hybrid cottonwoods. Oecologia 123, 82–89.

Miller, S.D., Cully Jr., J.F., 2001. Conservation of black-tailed prairie dogs (*Cynomys ludovicianus*). Journal of Mammalogy 82, 889–893.

Miller, B., Reading, R., Hoogland, J., Clark, T., Ceballos, G., List, R., Forrest, S., Hanebury, L., Manzano, P., Pacheco, J., Uresk, D., 2000. The role of prairie dogs as a keystone species: response to Stapp. Conservation Biology 14, 318–321.

Minchin, P.R., 1987. Simulation of multidimensional community patterns: towards a comprehensive model. Vegetation 71, 145–156.

Minchin, P.R., 1999. DECODA: Database for Ecological Community Data. Version 3.00 b06. Australian National University, Canberra.

Munn, L.C., 1993. Effects of prairie dogs on physical and chemical properties of soils. In: Oldemeyer, J.L., Biggins, D.E., Miller, B.J., Crete, R. (Eds.), Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. US Department of the Interior Fish and Wildlife Service, Washington, DC, pp. 11–17 Biological Report 13.

Oldemeyer, J.L., Biggins, D.E., Miller, B.J., Crete, R. (Eds.), 1993. Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. US Department of the Interior Fish and Wildlife Service, Washington, DC Biological Report 13.

O'Meilia, M.E., Knopf, F.L., Lewis, J.C., 1982. Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management 35, 580–585.

Parmelee, R.W., 1995. Soil fauna: linking different levels of the ecological hierarchy. In: Jones, C.J., Lawton, J.H. (Eds.), Linking Species and Ecosystems. Chapman & Hall, New York, pp. 107–116.

Parmenter, R.R., Parmenter, C.A., Cheney, C.D., 1989. Factors influencing microhabitat partitioning in arid-land darkling beetles (Tenebrionidae): temperature and water conservation. Journal of Arid Environments 17, 57–67.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchencko, J., Paine, R.T., 1996. Identifying keystone species is difficult but essential to understanding how loss of species will affect ecosystems. BioScience 46, 609–620.

Riddle, W.A., Crawford, C.S., Zeiton, A.M., 1976. Patterns of hemolymph osmoregulation in three desert arthropods. Journal of Comparative Physiology 112, 295–305.

Schmidt-Nielson, B., Schmidt-Nielson, K., 1950. Evaporative water loss in desert rodents in their natural environment. Ecology 31, 75–85.

Seastedt, T.R., 1984. The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology 29, 25–46.

Shalaway, S., Slobodchikoff, C.N., 1988. Seasonal changes in the diet of the Gunnison's prairie dog. Journal of Mammalogy 69, 835–841.

Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era? Biological Conservation 83, 247–257.

Slobodchikoff, C.N., 1983. Water balance and temperature preferences, and their role in regulating activity times of tenebrionid beetles. Oikos 40, 113–119.

Slobodchikoff, C.N., 1984. Resources and the evolution of social behavior. In: Price, P.W., Slobodchikoff, C.N., Gaud, W.S. (Eds.), A New Ecology: Novel Approaches to Interactive Systems. Wiley, New York, pp. 227–251.

Smith, G.A., Lomolino, M.V., 2004. Black-tailed prairie dogs and the structure of avian communities on the shortgrass plains. Oecologia 138, 592–602.

Stapp, P., 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands. Conservation Biology 12, 1253–1259.

Stewart-Oaten, A., Murdoch, W.W., Parker, K.R., 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology 67, 929–940.

Stewart-Oaten, A., Bence, J.R., Osenberg, C.W., 1992. The effects of unreplicated perturbations: no simple solutions. Ecology 73, 1396–1404.

Su, J.C., Debinski, D.M., Jakubauskas, M.E., Kindscher, K., 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for course-filter conservation. Conservation Biology 18, 167–173.

Vogel, S., Ellington Jr., C.P., Kilgore Jr., D.L., 1973. Wind-induced ventilation of the burrow of the prairie dog, *Cynomys ludovicianus*. Journal of Comparative Physiology 85, 1–14.

Weltzin, J.F., Archer, S., Heitschmidt, R.K., 1997a. Small-mammal regulation of vegetation structure in a temperate savanna. Ecology 78, 751–763.

Weltzin, J.F., Downhower, S.L., Heitschmidt, R.K., 1997b. Prairie dog effects on plant community structure in southern mixed-grass prairie. Southwestern Naturalist 42, 251–258.

Whicker, A.D., Detling, J.K., 1988. Ecological consequences of prairie dog disturbances: prairie dogs alter grassland patch structure, nutrient cycling, and feeding-site selection by other herbivores. BioScience 38, 778–785.

Whicker, A.D., Detling, J.K., 1993. Control of grassland ecosystem processes by prairie dogs. In: Oldemeyer, J.L., Biggins, D.E., Miller, B.J., Crete, R. (Eds.), Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. US Department of the Interior Fish and Wildlife Service, Washington, DC, pp. 18–27 Biological Report 13.

Whicker, A.D., Tracy, C.R., 1987. Tenebrionid beetles in the shortgrass prairie: daily and seasonal patterns of activity and temperature. Ecological Entomology 12, 97–108.

Wimp, G.M., Martinsen, G.D., Floate, K.D., Bangert, R.K., Whitham, T.G., 2005. Plant genetic determinants of arthropod community structure and diversity. Evolution 59, 61–69.

Wright, J.P., Jones, C.G., Flecker, A.S., 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132, 96–101.

SPECIES ASSESSMENT FOR BLACK-TAILED PRAIRIE DOG (*CYNOMYS LUDOVICIANUS*) IN WYOMING

prepared by

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Introduction

Prairie dog colonies once stretched from southern Canada to northern Mexico, east of the Rocky Mountains (Hall 1981). Prairie dogs affect many ecosystem processes (Detling and Whicker 1987) and studies have suggested that prairie dogs are important for the maintenance of biodiversity in grasslands (Miller et al. 1994, Reading and Matchett 1997), increasing species richness or abundance of plants (Bonham and Lerwick 1976, Whicker and Detling 1988), arthropods (Agnew et al. 1987), and vertebrates (Agnew et al. 1986, Barko 1996, Ceballos et al. 1999).

Historically, prairie dogs were the target of widespread eradication programs (Anderson et al. 1986, Miller et al. 1996), which, along with land conversion, led to decline of the species to less than 2% of its original range, by conservative estimates (Miller et al. 1994, Mulhern and Knowles 1995). Competition between livestock and prairie dogs for forage has long been the justification for eradication programs (Collins et al. 1984). However, O'Melia et al. (1982) found no significant difference in weight gain between steers that grazed on or off prairie dog colonies. In fact, facilitation in the form of enhancement of forage quality for, and preferential grazing by, pronghorns (Krueger 1986), bison (Coppock et al. 1983b, Krueger 1986) and domestic cattle (Knowles 1986) have been shown for prairie dog colonies relative to uncolonized mixed grass prairie. Despite the obvious reduction in above-ground biomass available for grazers caused by prairie dogs (Coppock et al. 1983a), ungulates seek out prairie dog colonies to forage (Whicker and Detling 1988). The advantage to grazers comes in the form of enhanced crude protein (nitrogen) content of the newly regrowing shoots of previously clipped vegetation (Detling and Whicker 1987, Sharps and Uresk 1990). Likewise, prairie dogs may maintain an herbaceous cover in grasslands and prevent encroachment of woody species, improving rangelands for other grazers (Weltzin et al. 1997a, Weltzin et al. 1997b).

Natural History

Morphological Description

Black-tailed prairie dogs (*Cynomys ludovicianus*) are robust, stockily built ground squirrels. These animals are usually a buff brown with a grizzled black appearance (Figure 1). The last third of the tail is black tipped and 7-10 cm long. Adult *C. ludovicianus* usually weigh 0.8-1.5kg and reach a length of 31-41cm (including the tail; Clark and Stromberg 1987). The head is broad and rounded with relatively large eyes and small ears. The legs are short and powerful, each foot having 5 digits with well-developed claws for digging. The skull characteristics of black-tailed prairie dogs are described by Hoogland (1996) and Hall (1981), but in general the skull is broad and angular with large processes (Figure 2). Their body pelage molts seasonally (twice yearly; Hoogland 1996) and is different between age and sex groups. The first to undergo the molt are the non-breeding juveniles, second are the non-breeding adults, third are the breeding males, and last are the breeding females (Hoogland 1995). It is thought that this sequence of molting is related to the overall body condition, with the most “fit” individuals molting first (Hoogland 1995). Juveniles undergo a “post-juvenile” molt starting at the rump and extending anteriorly (Smith 1967). Contrastingly, adults will molt posteriorly from the head every October. Males and females will also exhibit a differential molt, with the genitalia and secondary sexual characters molting soon after the head (Smith 1967). The color pattern on individual hairs differs during the respective molt period (Hoogland 1996).

All five species of prairie dogs (see Taxonomy) are similar in morphology and appearance, but since the species’ ranges do not overlap, locality is diagnostic (see below; Hoogland 1995).

Taxonomy and Distribution

Taxonomy

The complete taxonomic classification for the black-tailed prairie dog is as follows (Hoogland 1996): Order: *Rodentia,* Suborder: *Sciurognathi,* Family: *Sciuridae,* Subfamily: *Sciurinae,* Tribe: *Cynomyini,* Subtribe: *Spermophilina,* Genus: *Cynomys,* Subgenus: *Cynomys,* Species: *ludovicianus.* Two subspecies of black-tailed prairie dogs are recognized: *C. l. arizonensis* located in the southern portion of the black-tailed prairie dog range and *C. l. ludovicianus* located in the northern part of the black-tailed prairie dog range (Hall 1981; Hoogland 1996). Black-tailed prairie dogs are one of five species in the genus *Cynomys*, in the family *Sciuridae*. Mexican prairie dogs (*C. mexicanus*) are the closest relative to black-tailed prairie dogs but do not overlap in range. White tailed prairie dogs (*C. leucurus*) and Gunnison's prairie dogs (*C. gunnisoni*) are found in intermountain basins of the rocky mountain west (Clark 1987). Utah prairie dogs (*C. parvidens*) are found in short-grass prairies of southwestern Utah and are more closely related to white tailed prairie dogs (Hoogland 1996).

Interestingly, the prairie dog was originally named the "Louisiana marmot" (*Arctomys ludovicianus*) by Ord in 1815 due to its outward resemblance to a marmot, but the name was changed to the current genus *Cynomys* in 1817 by Rafinesque (Smith 1967).

Distribution

Black-tails are the most widely distributed species of prairie dog (Figure 3), thought to once occur from southern Canada to northern Mexico, covering a continuous 400-mile wide band from the foothills of the Rockies to the central lowlands of the Great Plains (Koford 1958, Hall 1981). Currently, this species still occurs over its entire range (except Arizona) in small, fragmented colonies (VanPutten and Miller 1999). Generally, *C. ludovicianus* occur east of the other four prairie dogs in North America, occupying more mesic habitats.

In Wyoming, the distribution of prairie dogs is restricted to the eastern third of the state, where short and mixed grass prairies dominate the landscape (Figure 4). The western extent of this range is not well defined, and there may be a zone of sympatry between *C. ludovicianus* and *C. leucurus*, which occupy the sage-grassland basins in central and western Wyoming. There is only one documented occurrence of a stable black-tailed prairie dog colony west of this area, in the Bighorn Basin. Since this colony is so far from the main range of black-tails and is located along a main highway, it likely represents an artificial, anthropogenic introduction rather than a legitimate range expansion (D. Keinath, personal communication).

Recently the Wyoming Game and Fish Department (WGFD) in cooperation with the Wyoming Bureau of Land Management (BLM) have completed a digital map of *C. ludovicianus* towns in Wyoming using 2002 aerial photographs. The portion of this map that represents active towns is unknown, since no estimate of activity has been assessed for the digitized towns. In addition, the map is incomplete since 1/3 of the photographs were unable to be digitized. In fall 2005, the map should be available on the Wyoming Natural Diversity Database (WYNDD) website (http://uwadmnweb.uwyo.edu/wyndd) after it has been evaluated and the quality of the map can be reported (D. Keinath, personal communication).

Habitat Requirements

General

Black-tailed prairie dogs are thought to have once covered the entirety of the Great Plains grasslands (Hall 1981, Miller et al. 1994) (Figure 5). Short- and mixed-grass prairies are easily colonized by prairie dogs especially when the range is overgrazed or in poor condition (Koford 1958). Tall-grass prairie appears to be difficult for prairie dogs to inhabit (Allan and Osborn 1954), possibly because the high levels of vegetative production interfere with clipping, a behavior used by prairie dogs to lower overall vegetative height, facilitating predator detection. Fine, non-sandy soils seem to be important for burrow construction (Clippinger 1989, Reading and Matchett 1997) and may influence the distribution of prairie dogs. Shrubby areas are less favorable for colony establishment, but may not inhibit expansion of existing colonies (Weltzin et al. 1997a). Gently sloping areas (0-10 degrees) are preferred and slopes over 20 degrees are rarely used in the establishment of new colonies (Clippinger 1989, Reading and Matchett 1997). *Cynomys ludovicianus* is rarely found above 2,377m and usually found below 1,829m (May 2004). Black-tailed prairie dogs do not require open water (Clippinger 1989) because of a specialized kidney physiology (Harlow and Menkens 1986) that allows them to more efficiently use water obtained from plants. There is no seasonal variation in habitat requirements due to the colonial nature of this species; therefore, the breeding, foraging, and over-wintering habitats are similar (Hoogland 1995).

A habitat suitability index (H.S.I.) model was completed in 1989 for black-tailed prairie dogs by the USFWS (Clippinger 1989). Models, such as the one developed by Clippinger (1989), have identified important habitat attributes for the species of interest. The habitat attributes considered by Clippinger (1989) were availability of food, water, cover, and soil type. His conclusions about food was that suitable habitat must contain sufficient grasses for spring and summer consumption, a forb flora which will be utilized in fall, and adequate prickly pear available for water needs during winter. According to Clippinger (1989), the food component of the H.S.I. model needs to be a minimum of 15% herbaceous cover for continuous habitation by prairie dogs. For the cover component, vegetative height levels of 5cm to 20cm are considered optimal with a slope of less than 10 degrees for burrow establishment. The cover values are considered to be the most critical component of the model by Clippinger (1989). Soil type is also considered, and has a broad spectrum of acceptable soil types for burrow establishment. Clippinger's (1989) H.S.I. equation is the following:

$$(V_1 \times V_2 \times V_3 \times V_4)^{1/4} = H.S.I.$$

Where: V_1= % herbaceous cover, V_2= slope, V_3= vegetative height, and V_4= soil type

In Wyoming, short-grass prairies in the southeast along with mixed-grass prairies through the northeast compose the majority of habitat for *C. ludovicianus* (Figure 4). The productive, gently rolling hills of the eastern third of the state provide the necessary habitat for colony establishment. The climate in Wyoming is favorable for year round activity, and provides a plant species composition and productivity comparable to that of the nationwide range.

Area Requirements

Coteries, the smallest family unit of a colony or town, are on average 0.3 ha in size, but can range from 0.05 ha to 1.0 ha in size (Hoogland 1995). In theory, the smallest possible unit of area prairie dogs could colonize would be the area of land needed for one breeding pair or family unit which would be ~ 0.05 ha. In Colorado, studies indicated that *C. ludovicianus* colony sizes ranged from one acre to 4,129 acres, with an average size of 75acres; however, most colonies were 1 – 20 acres in size (see May 2004).

Landscape Pattern

The general landscape pattern needed for continous habitation of black tailed prairie dogs is typified by the gently rolling topography and abundant forage of the Great Plains. Shrub dominanted landscapes can also be colonized, but are less preferred to open habitats of grasses and forbs (Clippinger 1989).

Movement and Activity Patterns

Dispersal

The most common movement of this species is of minimal distance due to its colonial nature. However, long distance dispersal does occur, but is very difficult to track (Hoogland 1995) and seems to be rarely successful due to predation risk away from the colony. A study conducted on intercolonial dispersal by Garrett and Franklin (1988) found that dispersal distances can be as much as 5 km. They also found that prairie dogs rarely disperse to start a new colony, rather they move to another established colony. The most common time for dispersal to occur is about a month or so after the juveniles have emerged for the year (Hoogland 1995).

The ultimate cause of dispersal from the natal breeding sites is to prevent inbreeding (Felhamer et al. 2004). Within *C. ludovicianus* populations, young males leave the family group before breeding, whereas females remain. In addition, adult males usually leave groups before their daughters mature (Hoogland 1982). Immigration and emigration by yearling males can be important for gene flow (outbreeding) in large complexes of black-tailed prairie dogs if dispersal is across mostly colonized area (Hoogland 1995).

Impediments to dispersal are largely centered on predation risk. Black-tailed prairie dogs heavily rely on the alarm calling actions of nearby vigilant conspecifics (Hoogland 1981), and a low degree of visual obstruction to detect danger. When venturing into uncolonized, unclipped territory, the danger of predation increases (Hoogland 1995). As a result, most adult and some juvenile male dispersal is within his home colony, although not near his home coterie. Long distance dispersal, when it occurs, is most commonly associated with juvenile rather than adult males, and is usually solitary rather than group movements. Male dispersal peaks during a postweaning period (June – August; Roach et al. 2001). Dispersal of juvenile females is very uncommon because they usually stay and breed on the home coterie for life. If dispersal does occur with a female prairie dog, it is almost always long distance dispersal to another established colony (Hoogland 1995). Other barriers to movement are few, but include large bodies of water such as wide rivers and large lakes.

Activity Patterns

Prairie dogs are diurnal, usually appearing above ground at dawn during the warmer months and midmorning during the winter months. The heaviest above ground activity occurs between 7am and 11am and 5pm and 8 pm (Tileston and Lechleitner 1966, Biggins et al. 1993). *Cynomys ludovicianus* may spend as much as 95% of their time above ground during the daylight hours, and retreat into burrow for only 15-20 minutes to momentarily escape the heat (Hoogland 1995).

Black-tailed prairie dogs are not “obligate hibernators”; instead, they exhibit a state of facultative torpor due to food shortage (in captivity) during the winter months (Harlow and Menkens 1986) and/or weather (i.e., ambient temperature for free-ranging *C. ludovicianus*; Lehmer et al. 2001, 2003). Free-ranging females demonstrated facultative aestivation in summer months during periods of precipitation (Lehmer et al. 2003). Although *C. ludovicianus* demonstrate facultative torpor, they can be active throughout the year (Hoogland 1995). Facultative torpor is one area of prairie dog physiology and ecology that needs further study.

Reproduction and Survivorship

Breeding Behavior

Black-tailed prairie dogs exhibit a harem-polygynous mating system (Hoogland et al. 1987). Usually, one breeding male, two to three adult females, and one or two yearlings of each sex make up a territorial family group, or coterie, although as many as 26 prairie dogs may occupy the largest of coteries (Hoogland 1995). Fierce protection of coteries by males can lead to combat between males, but rarely leads to serious injury or death. Coterie size may vary from 0.05 to 1.1

ha and will contain a variable number of burrows depending on the number of animals, especially breeding females, on that coterie. Since prairie dog females usually stay on the natal coterie, this species avoids inbreeding by four mechanisms: 1) male biased natal dispersal, 2) older males disperse from coteries when daughters become sexually mature, 3) yearling females are unlikely to come into estrus when their father is on the colony, and 4) behavioral avoidance of mating with kin. These mechanisms are further explained in Hoogland (1995).

Breeding Phenology

The breeding season of black-tailed prairie dogs occurs between late January and early April (Clark and Stromberg 1987) and lasts for 2-3 weeks (Smith 1967). Timing of copulation is probably dependant on food availability and the severity of the preceding winter (Koford 1958, Smith 1967). Black-tailed prairie dogs are generally synchronized breeders (Hoogland 1981), breeding the same day in a coterie, and perhaps over 5 days throughout the colony (Hoogland 1995). Gestation is between 28 to 32 days (Smith 1967, Clark and Stromberg 1987). Altricial young are usually born in the early spring and emerge from burrows at about 6 weeks of age. Pups are fully grown in about 90 days (Clark and Stromberg 1987). Latitudinal differences in time of breeding are also evident; for example, *C. ludovicianus* in Texas and Oklahoma breed in January, in Colorado during February, and in Montana during March (Hoogland 1995, 1996).

Fecundity and Survivorship

Sexual maturity does not occur until 2 years of age (Smith 1967) differing from white tail prairie dogs which mature and breed at 1 year of age. Garrett et al. (1982) found that the age of first reproduction and pregnancy rate were both affected by the availability of food, and Knowles (1987) found that litter size is directly connected to precipitation level of the preceding year. Additionally, (Koford 1958) stated that breeding success is not necessarily depressed in small groups as it is in other social organisms like colonial nesting birds. An average litter size is 4 (Anthony and Foreman 1951) to 5 pups (Clark and Stromberg 1987) with the range occurring between 2 and 8 (Hoogland et al. 1987).

Survivorship of male prairie dogs can be 3 or 4 years old and females usually live to be 5 or 6 years old (see Figure 6; Hoogland et al. 1987). Natal survivorship is unknown, but infanticide has been documented and is considered the major cause of juvenile mortality within colonies (Hoogland 1995, 1996). Juvenile survivorship does not appear to be as sex-biased as adult survivorship with about 50% of each sex surviving their first year (Hoogland 1995).

Population Demographics

Metapopulation Dynamics

Although immigration and emigration to and from neighboring colonies is not important in maintaining genetic diversity (see below), maintaining corridors between distinct colonies is important for the long-term persistence of a metapopulation. A metapopulation can persist as long as rate of recolonization (i.e., after events such as plague eliminates a colony) exceeds rate of extinction. Increased isolation and disconnectivity of colonies will decrease successful dispersal between colonies, increase genetic diversity between colonies, and may decrease genetic diversity within isolated colonies through possible inbreeding and overall loss of alleles. Movement between existing or unoccupied colonies is affected by physical aspects of the surrounding landscape, such as tall grasses or urban and agricultural development. Maintaining corridors such as drainages, roads, or trails could facilitate recolonization of unoccupied colonies and continual dispersal among colonies (Roach et al. 2001).

Genetic Concerns

Dobson et al. (2004) demonstrated that the polygynous mating system (coteries within colonies) and female philopatry (see Dispersal below) of *C. ludovicianus* results in a strong genetic differentiation of coteries within a colony. This genetic substructure within a colony has a conserving influence on genetic diversity because different alleles predominate in different coteries, and decrease the loss of genetic diversity of the entire colony. In fact, the genetic diversity within a colony was influenced more from coteries within the colony than immigrants (males) from neighboring colonies. Translocation of females (essentially increasing the female dispersal rate) could actually increase the rate of inbreeding and loss of genetic variation by bringing related males and females into spatial proximity (Sugg et al. 1996, Dobson et al. 2004). This information should be considered when reintroducing or relocating *C. ludovicianus* to different colonies.

Food Habits

Cynomys ludovicianus is herbivorous, consuming the stems, leaves, seeds, and roots of various grasses, forbs, shrubs, and cacti. However, despite this breadth of food sources, black-tailed prairie dogs are not considered opportunists (Uresk 1984), apparently selecting for specific species of these growth forms. In fact, prairie dogs have been shown by Wydeven and Dahlgren (1982) and Fagerstone et al. (1981) to choose plants that are not abundant on the range colonized. Unlike other ground squirrels, and even other species of *Cynomys*, the black-tailed prairie dog does not store food in its burrow (Koford 1958) or hibernate during the winter.

The first known food habit study (Kelso 1939) found that western wheat grass (*Agropyron smithii*) and six-weeks fescue (*Festuca octoflora*) were most important followed by Russian thistle (*Salsola australus*), prickly pear cactus (*Opuntia* spp.) and saltbush (*Atriplex* spp.). Uresk (1984) found that only four plant species composed 65% of the diet of black-tails in South Dakota, of which grasses accounted for 87% of the diet and forbs composed 12%. Summers and Linder (1978), as well as Fagerstone et al. (1981) and Wydeven and Dahlgren (1982) also found that grasses are the most important component of prairie dog spring and summer diets, sometimes composing up to 90% of the food eaten.

Much controversy has arisen on the food habits of prairie dogs due to the potential for competition with domestic cattle (Uresk and Bjugstad 1983). However, steer weight gain on pastures with and without prairie dog grazing were not statistically significant (O'Melia et al. 1982, Uresk and Bjugstad 1983). Further, preferred plant species overlap between cattle and prairie dogs is not significant (Knowles 1986). Studies of the grazing relationship between bison (*Bison bison*) (Coppock et al. 1983b, Krueger 1986), pronghorn (Krueger 1986), and cattle (Knowles 1986) suggest that prairie dogs increase nutritional value of forage and change grazing habits by increasing shoot nitrogen and reducing standing dead biomass (Detling and Whicker 1987).

Seasonal change in diet is very common and is thought to occur in response to the decreased crude protein and increased fiber of mature plants (Fagerstone et al. 1981). Koford (1958) and Fagerstone et al. (1981) found that during winter, basal parts of buffalograss (*Buchloe dactyloides*), prickly pear cactus, fourwing saltbush (*A.canescens*), and rabbitbrush (*Chrysothamnus* spp.) were important. Shallow digging for roots may also be an important source of protein during winter (Tileston and Lechleitner 1966). During spring, the newly greening vegetation is preferred and the dominant species consumed are Russian thistle, scarlet globemallow (*S. coccinea*) and summercypress (*K. scoparia*). Shifts from C_3 to C_4 plants throughout the summer may occur in response to the subsequent greening of these species. During fall, the green bases of grasses such as buffalograss and blue grama (*Bouteloua gracilis*) are sought (Koford 1958, Fagerstone et al. 1981). Winter food items include mostly roots and prickly pear cactus (Summers and Linder 1978, Wydeven and Dahlgren 1982). Interestingly, prairie dogs have apparently developed the necessary physiology to cope with the oxalic acid occurring in prickly pear, in order to gain its moisture rich benefit in the winter diet (Fagerstone et al. 1981). It has been suggested that prairie dogs choose the most succulent form of vegetation available on a seasonal basis due to water stress (Fagerstone et al. 1981). Grass may compose as much as 85% of its wet weight as water (Hansson 1971), thus providing prairie dogs with the water needed for efficient assimilation (Becksted 1977).

Community Ecology

The potentially disproportionate influence of black-tailed prairie dogs in prairie ecosystems has led their being called keystone species, but this designation has been contentious (Stapp 1998; Miller et al. 2000). Prairie dogs (*Cynomys* spp.) are important members of grassland communities. They affect rangeland habitats by influencing plant species diversity and composition, creating habitat preferred by other wildlife species (May 2004). An estimated 170 vertebrate species have been alleged to rely on prairie dogs for some life needs (Clark et al. 1982; Reading and Matchett 1997; Lomolino and Smith 2003b). Well known obligates of prairie dog colonies include black-footed ferrets (*Mustela nigripes*) (Biggins et al. 1985, Reading 1993) and burrowing owls (*Athene cunicularia*) (Tyler 1968, Sharps and Uresk 1990), both of which depend on prairie dogs for burrow structures and/or food.

Prairie dogs are thought to affect many ecosystem processes (Detling and Whicker 1987) and habitat characteristics (Weltzin et al. 1997b), thereby having direct and indirect influences on the flora and fauna around them. For example, the black-tail's practice of "clipping" tall vegetation from burrow entrances to increase predator detection is similar to grazing and burning rangeland practices that encourage new plant growth, which is more nutritional and palatable to other wildlife species and domestic livestock (Knight 1994; May 2004). Removal of this species from prairie ecosystems could have effects on plant and animal species diversity and abundance over time. Lomolino and Smith (2003b) determined that *C. ludovicianus* towns harbored more rare and imperiled species (i.e., swift fox, black-footed ferrets, and burrowing owls), and therefore a decrease in prairie dogs could be detrimental to these species.

Conservation

Conservation Status

Federal Endangered Species Act

In 1998, two petitions were received by the U.S. Fish and Wildlife Service (USFWS) to list *C. ludovicianus* as threatened under the Endangered Species Act of 1973 (ESA). One petition was filed on July 30, 1998 by the National Wildlife Federation (NWF), and the second petition was received on August 26, 1998 from the Biodiversity Legal Foundation, the Predator Project, and Jon C. Sharps (see USFWS 2004b). These petitions listed several factors that could be major threats to the viability and conservation of *C. ludovicianus*, including habitat loss, habitat fragmentation, disease, unregulated shooting and poisoning, and the synergistic effects of these threats and others. The 90-day finding for the petitions was published in the Federal Register (FR) on March 25, 1999 (USFWS 1999) which stated that the petition action may be warranted. The 12-month finding by the USFWS on February 4, 2000 announced that listing *C. ludovicianus* was warranted but precluded (USFWS 2000), and therefore considered a candidate for listing.

Four of the five necessary conditions for listing were demonstrated (all were met except #2) (VanPutten and Miller 1999). These conditions were:

1. Present of threatened destruction, modification, or curtailment of habitat.
   This condition for listing was met by demonstrating the limiting of habitat, and reduction of populations, that has occurred largely due to agricultural interests.
2. Over-utilization for commercial, recreational, scientific, or educational purposes.
   This condition was not met. However, recreational shooting of prairie dogs may be reinvestigated in the future, depending on regulation of this activity by agencies.
3. Disease or predation
   This condition was met due to the high mortality (99.9%+) of prairie dogs faced with sylvatic plague. Unfortunate epizootics could easily eliminate the population.
4. Inadequacy of existing regulatory mechanisms
   This condition was met due to the classification of prairie dogs as pests in the states in which they occur. Adequate management actions to curtail recreational shooting and poisoning do not exist for many states.
5. Other natural or man-made factors affecting its continued existence.
   This condition was met due to reasons in #4.

Candidate listing required reassessments and resubmitted petitions to be listed annually in the FR (see USFWS 2001, USFWS 2002, USFWS 2004a). From these assessments and available scientific and commercial information it was determined that the petitioned action to list *C. ludovicianus* under the provisions of the Endangered Species Act (ESA) was not warranted on August 18, 2004. As a result, *C. ludovicianus* is no longer considered a candidate for listing (USFWS 2004b). The action to remove *C. ludovicianus* from the ESA candidate list was based on the following determinations: 1) destruction of habitat from agricultural conversion and other factors was no longer a threat, 2) modification of habitat due to the presence of plague was a moderate, imminent threat, 3) the present limitation of habitat due to chemical control was no longer a threat, 4) effects due to scientific or education purposes and commercial use of the species via the pet trade were not threats, 5) recreational shooting could be a low, imminent threat in some circumstances, 6) predation was not a threat, 7) disease was a moderate imminent threat, 8) the inadequacy of existing regulatory mechanisms was a moderate, imminent threat, and 9) chemical control and synergistic effects were moderate imminent threats (USFWS 2004b).

Bureau of Land Management

The State Offices of the Bureau of Land Management (BLM) in Montana, New Mexico, North Dakota, South Dakota, and Wyoming list *C. ludovicianus* on their sensitive species lists. According to the BLM Manual 6840, this designation is meant to provide protection of *C. ludovicianus* and the habitat on which they depend. Therefore the BLM is responsible for reviewing programs and activities on BLM land to determine their potential effect on *C. ludovicianus* (USDOI BLM Wyoming 2001; Keinath et al. 2003).

Forest Service

The range of *C. ludovicianus* encompasses portions of four forest service regions: the central part of the Northern Region (R1), the eastern half of the Rocky Mountain Region (R2), the eastern portion of the Southwestern Region (R3), and the western portion of the Southern Region (R8). Currently *C. ludovicianus* is listed as a sensitive species in Region 2 (http://www.fs.fed.us/r2/projects/scp/) and the subspecies, *C. l. arizonensis* is listed in Region 3 (New Mexico and Arizona; BISON 2004a).

State Wildlife Agencies

The Wyoming Game and Fish Department (WGFD) has developed a matrix of habitat and population variables to determine the conservation priority of all species in the state. Seven classes of Native Species Status (NSS) are recognized, with NSS1 representing critically imperiled species and NSS7 representing stable or increasing species. Classes 1, 2, 3, and 4 are considered to be high priorities for conservation attention. The WGFD assigns *C. ludovicianus* a special concern rank of NSS3. The NSS3 rank is based on WGFD estimates that *C. ludovicianus* populations in Wyoming are declining or restricted in numbers and/or distribution and habitat is restricted and/or vulnerable to human disturbance (Oakleaf et al. 2002; Keinath et al. 2003). Oklahoma also recognizes *C. ludovicianus* as a special management concern. See Table 2 for a complete list of state designations for *C. ludovicianus* across its range.

Heritage Ranks and WYNDD's Wyoming Significance Rank

The Natural Heritage Network assigns range-wide and state-level ranks to species based on established evaluation criteria (e.g., Keinath and Beauvais 2003, Keinath et al. 2003). *Cynomys ludovicianus* merits a global rank of G3 (averaged), which means that when the range-wide population is considered, it is deemed by Heritage scientists as rare or local throughout its range or found locally in a restricted range. This is based on evidence that the extent of occupied habitat and abundance has been reduced from its historic range (NatureServe 2004).

Twelve western states and provinces have assigned a State Rank to *C. ludovicianus*, none of which rank it as demonstrably secure (Figure 7). In general, state ranks are assigned based on the assessed risk of extinction within a state, where S1 species are deemed critically imperiled and S5 species are deemed demonstrably secure. These assessments are based on the biological information on population status, natural history, and threats at the state level. *Cynomys ludovicianus* is ranked as imperiled (S2) in New Mexico, Wyoming, and Saskatchewan; vulnerable (S3) in Kansas, Montana, Oklahoma and Texas; and apparently secure (S4) in Colorado, Nebraska and South Dakota. They are presumed extirpated (SX) in Arizona and their status is under review in North Dakota (SU) (NatureServe Explorer 2004; Keinath et al. 2003, Keinath and Beauvais 2003). The black tailed prairie dog was ranked as imperiled in Wyoming due to the following factors pertaining mainly to large towns (Keinath et al. 2003):

- Their range encompasses a moderate proportion (between 10% and 50%) of the state. Their historic range in Wyoming likely covered about 40% of Wyoming (Clark and Stromberg 1987). However, given fragmentation of habitat suggesting 0.01% of this historic range being occupied (Table 1), prairie dogs may actually cover less than 240,000 acres, or 0.004% of the state (e.g., Luce 2001). Wyoming likely contains about 17% of the historic black-tailed prairie dog range.
- They exhibit low range occupation (<20% of delineated range) and a patchy range-wide distribution. Historic distribution touches several states, including Montana, Wyoming, North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Texas, New Mexico, Arizona, and Colorado, but is quite patchy within this range.
- Their abundance within Wyoming is uncertain but probably declining (due to the intrinsic vulnerabilities and external threats noted below). At the turn of the century, black-tailed prairie dogs occupied more than 40 million acres, but estimates suggest less than 1% of that area is currently occupied (Merriam 1902 as cited in Van Putten 1999; Van Putten and Miller 1999). The area of occurrence is now very patchy (Mulhern and Knowles 1995). In Wyoming about 0.01% of historically occupied land contains currently active colonies (Luce 2001), which correlates to about 600,000 acres. However, estimates of active towns are al low as 130,000 acres (Mulhern and Knowles 1995).
- They have high intrinsic vulnerability due to habitat specificity and susceptibility to disease. Black-tailed prairie dogs are habitat specialists that occur mainly in flat, short and mixed-grass prairies with fine, non-sandy soils (e.g., Hall 1981;Miller et al. 1994; Clippinger 1989). Further, they are very susceptible to plague (*Yersinia pestis*), and Wyoming seems to be experiencing a statewide epizootic as of summer 2001 (personal communications with state land managers).
- They face high extrinsic threats, including active eradication programs, land conversion, and habitat fragmentation. Poisoning, shooting, land conversion can each be a substantial threat to black-tailed prairie dogs, but when combined they can devastate entire populations beyond the point of recovery (e.g. Luce 2001; Gilpin 1999).

The black-tailed prairie dog's Wyoming Contribution Rank is "high," because it is a native resident with a moderate proportion of its otherwise restricted continental range in Wyoming. Further, it has a restricted and patchy continental distribution and is arguably more secure in Wyoming relative to other states (Keinath et al. 2003, Keinath and Beauvais 2003).

Biological Conservation Issues

Abundance and Abundance Trends

No good estimate of *C. ludovicianus* abundance across its range is available, although it is estimated to be in the millions. Abundance of *C. ludovicianus* is generally expressed in terms of surface area (hectares/acres) occupied by their colonies (Miller and Cully 2001), as it is more cost-effective than surveying populations and calculating density. The USFWS believe that estimates of occupied habitat provide the best available and most reasonable means of gauging populations and status of the species across its range (USFWS 2004b). Ground-truthing exercises are currently being carried out in New Mexico, Oklahoma, Texas, and Wyoming; therefore, a better understanding of the accuracy obtained from using surface area occupied (obtained from aerial surveys) to estimate abundance will be gained (Luce 2003; USFWS 2004b). Using recent estimates of active *C. ludovicianus* acreage obtained from aerial and remote sensing surveys, estimates of *C. ludovicianus* abundance was calculated by multiplying each acre by the typical density of individuals per acre in colonies across its range (2 to 18 individuals per acre). From these calculations the most current estimated abundance of *C. ludovicianus* is between 3,684,000 and 33,156,000 (average 18,420,000; USFWS 2004b). At the beginning of the 19th century, *C. ludovicianus* numbered near five billion (see BISON 2004b). Thus the abundance of black-tailed prairie dogs has drastically decreased in the past century. It is estimated that *C. ludovicianus* has been reduced across its western range by about 98 – 99% of its former abundance (Wuerthner 1997).

In Wyoming, Mulhern and Knowles (1995) estimated that between 53,000 and 82,590 hectares were occupied by black-tailed prairie dogs. Estimates from 2003 indicate that *C. ludovicianus* occupy approximately 51,000 hectares, which conforms to the projected decline suggested by Wyoming Game and Fish Department as a result of plague-infested colonies (USFWS 2004b). In Wyoming, habitat loss or modification does not seem to be a large threat to *C. ludovicianus* populations, since very little habitat has been lost within the past 30 years (i.e., only 25,000 acres of rangeland converted to crops) and possible future land conversion is rather unlikely, since Wyoming's climate is not conducive to productive and economic crop growth (WBPDWG 2001). Please refer to Table 1 for a state-by-state account of occupied acreage and Table 2 for population trends throughout *C. ludovicianus* range.

Prior to 2003, most rangeland estimates of *C. ludovicianus* abundance were inconsistent and based on imprecise and cursory information, such as limited aerial surveys, review of available aerial photographs, and estimates from weed and pest control staff (Sidle et al. 2001; USFWS 2004b). These various methods provided incomplete and ad hoc data in order to determine abundance trends. For more valid estimates, methodologies across *C. ludovicianus* range need to be standardized. In addition, colonies need to be surveyed more regularly. Taking these actions will not only provide a more accurate estimate of abundance, but will also help document changes in populations as a result of plague, drought, and habitat alterations (see Inventory and Monitoring below).

Distribution and Connectivity Trends

At the turn of the 1900's black-tailed prairie dogs occupied more than 40 million nearly continuous hectares (Merriam 1902 as cited in Van Pelt 1999), and their range included portions of eleven States, Canada, and Mexico. Less than 1% of that area (< 324,000 ha) was occupied as of 1998 (VanPutten and Miller 1999). Despite the loss of habitat, *C. ludovicianus* are still widely distributed over their original range; although, they now occur in small, fragmented, isolated patches (Miller et al. 2000; USFWS 2004b). Arizona is the only state that the black-tailed prairie dog has been totally extirpated from its former range (Mulhern and Knowles 1995). Reduction in connectivity between colonies has probably had minor impacts on genetic diversity (see Roach et al. 2001, Dobson et al. 2004), but major impacts on recolonization success after serious population reductions (i.e., after plague or eradication efforts; see below).

Range contractions have been most evident in Arizona (now extirpated), western New Mexico, and western Texas through conversion of grasslands to desert shrub lands and in the eastern portion of *C. ludovicianus* range in Kansas, Nebraska, Okalahoma, South Dakota, and Texas through cropland development (USFWS 2004b). Most of the range reduction from agricultural development occurred in the early- to mid-1900s, and is a minimal threat today (see Extrinsic Threats).

The Interstate Black-tailed Prairie Dog Management Team plan states that Wyoming has a fraction (~ 0.01%) of the historical range currently occupied by active colonies (Luce 2003). In Wyoming, there is very little land under cultivation (< 5%), so the levels of land conversion observed in other parts of this species range have not impacted the species as severely. Competition with livestock ranching, and the control efforts that result (see Below), remains the main threat to further loss of species range. Landowner incentive programs may promote the use of some lands, currently used intensively for grazing, for prairie dog habitat.

Extrinsic Threats

The cause of *C. ludovicianus* population declines in the past century can be attributed to 1) intensive eradication programs, 2) agricultural conversion of rangelands, 3) sylvatic plague, 4) urbanization, and 5) recreational shooting. (Wuerthner 1997; Van Pelt 1999). The synergy of these threats may reduce populations drastically. The following section will address these issues. oisoning and shooting of prairie dogs by ranchers, and agricultural conversion of habitat are responsible for the majority of *C. ludovicianus* population decline (Miller et al. 1990, 1994)

Control Programs

Poisoning programs were initiated in the early 1900's when prairie dogs were first deemed an agricultural threat by Merriam (1902 as cited in Van Pelt 1999), with accusations that prairie dogs compete with domestic livestock for forage (Hoogland 1996). Both small-scale (i.e., trapping and drowning) and large-scale (i.e., poisoning and fumigation) eradication programs were used (Barko 1997). Since federal eradication programs were initiated in 1915, many federal land and wildlife management agencies, as well as state agencies, have been responsible for the extirpation of prairie dogs from millions of hectares (Anderson et al. 1986, Mulhern and Knowles 1995). In fact, it is thought that such poison eradication programs were responsible for the extirpation of *C. ludovicianus* in Arizona (see AGFD 1988). Despite modern evidence about grazing relationships (Coppock et al. 1983b, Uresk and Bjugstad 1983, Uresk 1984), and demonstration of the economic inefficacy of poisoning (Miller et al. 1996), this practice has continued into the 1990's with state and federal mandates. Though federal and state agencies have slowed poisoning in 1999 (WYGF 2001), private land owners are still permitted to exterminate prairie dogs from their lands. However, many states, including Wyoming, are developing incentive programs for private landowners to keep prairie dogs on their lands (WYGF 2001). Shooting also occurs for population control across the range of all 5 species in the U.S. (Mulhern and Knowles 1995). The USFWS (2004b) no longer consider control programs a threat to the persistence of *C. ludovicianus* populations across its range; chemical control programs and synergistic effects were considered a moderate imminent threat.

Recreational Shooting

Little is known about recreational shooting affects on *C. ludovicianus* populations; however, it is suggested that recreational shooting would only limit, not extirpate populations (Vosburgh and Irby 1998). Fox and Knowles (1995 in Mulhern and Knowles 1995) state that it would require one recreational day of shooting for every 6ha of prairie dogs to adversely affect populations. In addition, the USFWS (2004b) have found recreational shooting only a low, imminent threat, since it has been recognized that populations are capable of recovering from such adverse impacts. However, in some states, interest in recreational shooting has increased. Some States with large amounts of public land are experiencing increased shooting pressures on prairie dogs (USFWS 2004b). For example, in Wyoming, an increase in requests from the public as to where to shoot prairie dogs has been noted by Wyoming Game and Fish Department, Wyoming Department of Agriculture, and local Chambers of Commerce. This increased interest in prairie dog shooting, both locally and out-of-state has raised some concern that recreational shooting may become a significant contributor to *C. ludovicianus* population declines in Wyoming (WBTPDWG 2001). States concerned with increased recreational shooting are beginning to implement regulations to better monitor and control this activity (USFWS 2004b). Recently, Thunder Basin National Grassland has implemented a no shooting policy on 45,000 acres of prairie dog habitat in northeastern Wyoming (USDA 2004). This ban is one of the first of its kind on public lands. Other States, such as Arizona, Colorado, Montana, and South Dakota have also begun to restrict hunting on *C. ludovicianus* by limiting seasons and/or closing public lands. Still other States have begun to require hunting permits for public lands (Luce 2003). Shooting restrictions extended by some states on black-tails are a positive step; however, some researchers are concerned that it will cause a shift of shooting to the other species of *Cynomys* (VanPutten and Miller 1999).

Habitat Alterations

Reductions in *C. ludovicianus* habitat have occurred across its historical range, as a result of urban development and conversion of rangelands for agricultural purposes. Historically, it was conversion of short- and mixed-grass prairie for agriculture that was the major cause of populations decline, specifically in the eastern range of *C. ludovicianus* (Graul 1980, Dinsmore 1983). However, conversion of habitat from agricultural development is no longer deemed a threat to the persistence of *C. ludovicianus* (USFWS 2004b), since most of the arable land has already been converted (Mulhern and Knowles 1995). This reduced threat is in part a result of research by Sidle et al. (2001) that noted that vast areas of suitable habitat for colonization and expansion of this species still remain, as well as reports that estimate hundreds of millions of acres of potential habitat still remain intact (see USFWS 2004b and Table 1). Along the Front Range in Colorado, urbanization is considered one of the greatest threats to habitat loss (CBOS 1996; CDOW 2003). The USFWS (2004b) recognize that this may be a factor in habitat loss along the Front Range, but does not feel urbanization would present a substantial threat to *C. ludovicianus* across its entire range. In Wyoming, the population of Crook, Cambell, Johnson, Sheridan, and Laramie Counties has increased >10%, Weston, Converse, Platte, and Goshen Counties has increased by <10%, and the only county within *C. ludovicianus* range that has decreased, is Niobrara County (Miller 2001). The associated urban development with the population growth may become more of a threat to *C. ludovicianus* populations than has been present in the past.

Losses in extent and connectivity of native short- and mixed-grassland ecosystems of the Great Plains of North America have been drastic. Historically, *C. ludovicianus* range was continuous and covered >40 million hectares; however, over the past century, this habitat has been fragmented and reduced to less than 600,000ha (Miller and Cully 2001). Fragmentation of grasslands has occurred from such activities as agriculture, urban development (and its associated roads), and oil and gas development (Van Pelt 1999). As a result of this fragmented landscape, colonies have been isolated from one another, disrupting gene flow and successful distribution of dispersing males from their natal colony (Roach et al. 2001). Although habitat has been fragmented and some colonies isolated, it does not appear that this creates a great loss in genetic diversity (see Dobson et al. 2004). On the other hand, if populations are isolated from potential emigrating individuals, and the population within that colony is eliminated, it could become locally extinct. The USFWS (2004a) suggest that isolation of colonies may present a defense against the spread of plague, leaving some remnant populations unaffected and therefore do not deem habitat fragmentation an imminent threat to *C. ludovicianus* populations. In Wyoming, oil and gas development and population increase may become an issue, since suitable *C. ludovicianus* habitat is being developed (see Figure 8).

Although habitat loss appears to be a large threat to *C. ludovicianus* populations, it does appear that this species can adapt to various changes in their habitat. For example, Sidle et al. (2001) documented active *C. ludovicianus* colonies on small patches of grassland surrounded by agricultural development and near housing developments in Nebraska, and in the vicinity of roads and other developments in Wyoming.

Disease

Sylvatic plague (*Yersinia pestis*; known as Bubonic plague in humans) is an exotic bacterial disease that first entered the United States just before the turn of the century (Culley 1989). It was first discovered in the 1940’s in Texas (Cully et al. 1997). This disease has profound impacts on populations of prairie dogs (mortality ≥ 99%), which have little to no immunity. The plague can be especially devastating for isolated populations (see Wuerthner 1997). However, isolation of populations as a result of habitat fragmentation may be beneficial in preventing the spread of plague throughout entire metapopulations (see Habitat Alteration above). Plague not only has serious immediate effects, but long term population and demographic effects as well when coupled with shooting and poisoning. In fact the demographic changes imposed by such activities may place the species in an “extinction vortex” that the species may not recover from (Gilpin 1999). Populations west of the Dakotas commonly experience epizootics every 5-7 years (Culley, pers. comm.) and these outbreaks may hold the population level at about 40% of what it was before the epizootic (Knowles 1987).

Plague continues to be a threat to *C. ludovicianus* populations in Wyoming. Nearly all Wyoming populations of white and black-tailed prairie dogs have witnessed declines due to plague outbreaks since the 1930’s (WBTPDWG 2001). It is suspected that the plague is responsible for population declines in Wyoming (see Abundance Trends). Important locations of extensive black-tailed colonies, such as Thunder Basin National Grassland, have experienced losses of up to 70% of the total active acreage due to plague epizootics (T. Byer, personal communication).

The movement and maintenance of plague is not well understood (Anderson and Williams 1997) and needs further research. However, it has not yet expanded to cover the species national range. The occurrence of *Y. pestis* is generally west of the Dakotas; however, new reports indicate steady eastward movement in the southern part of the range, into Kansas (Cully et al. 2000). It is thought that the disjunctive and patchy distribution of *C. ludovicianus* populations throughout its range has prevented the devastating affects of plague on populations (WBTPDWG 2001).

Although the USFWS (2004b) considers plague the most important factor influencing black-tailed prairie dogs, they still only view plague as a moderate, imminent threat. They base their findings on the following information: 1) high exposure doses of plague bacilli may be necessary for disease contraction in some individuals, 2) limited immune response has been observed in some individuals, 3) a population dynamic may have developed in low-density isolated populations that contributes to the persistence of these populations, 4) the apparent ability of some sites to recover pre-plague levels after a plague epizootic, and 5) approximately one-third of the species' historic range has not been affected by plague.

Other

Predation of prairie dogs by coyotes (*Canis latrans*), badgers (*Taxidea taxus*), black footed ferrets (*Mustela nigripes*), bobcats (*Lynx rufus*), rattlesnakes (*Crotalis* spp), bullsnakes (*Piuophis melanoleucus*), golden eagles (*Aquila chrysaetos*), prairie falcons (*Falco mexicanus*), and accipiter and buteo hawks (*Accipiter* sp. and *Buteo* sp.) has occurred for as long as these species have inhabited the Great Plains. It is unlikely that these predators present a significant population threat to the species on their own (Hoogland 1981, 1996; WBTPDWG 2001). In addition, coloniality and antipredator calls offer a great predator detection system to minimize predation loss (Linner 2001). However, human predation in the form of recreational shooting may be an important adverse factor (see Recreational Shooting above), since recreational hunting can remove many individuals each day and change the demographic structure of metapopulations (Knowles 1987).

Invasive plant and animal species (other than plague, discussed below) do not appear to be a problem affecting prairie dog abundance or distribution.

Intrinsic Vulnerability

Habitat Specificity and Fidelity

Black-tailed prairie dogs occupy short- and mixed-grass prairie ecosystems, which can vary with respect to plant species composition, soil type, and topography (see Habitat). However, due to the colonial nature of *C. ludovicianus*, high fidelity for their habitat, once selected, is demonstrated. A loss of utilized habitat may cause populations to decrease.

Territoriality and Area Requirements

Within colonies, family groups (coteries) are extremely territorial defending their territory from other coteries (Hoogland 1995). Coterie's territories usually occupy about one-third of a hectare (Hoogland 1996); however, coteries occupying areas as large 1.01 hectares have been documented (Hoogland 1995). Since individuals of a coterie obtain 99% of their food and other resources within their territory, size and habitat quality is important (Hoogland 1995). Hof et al. (2004) estimated that one hectare could successfully maintain 18.4 individual prairie dogs. However, this number may be high for Wyoming. For example, when compared with other states within *C. ludovicianus* range, it appears that populations within Wyoming require larger tracts of land per colony, averaging 13 – 764 hectares per colony (see Clark et al. 1982). Fragmentation that reduces habitat availability may be detrimental to the populations.

Susceptibility to Disease

Although coloniality is thought to benefit communities of *C. ludovicianus* (i.e., predator detection), coloniality also promotes the spread of disease, which could significantly suppress local populations (Linner 2001). For example, sylvatic plague (*Yersinia pestis*), an exotic bacterial disease that first entered the United States just before the turn of the century (Culley 1989), has profound impacts on populations of *C. ludovicianus* (mortality ≥ 99%), which have no immunity. Plague can spread across whole *C. ludovicianus* complexes in just a few years (e.g., Anderson and Williams 1997, Cully and Williams 2001). Plague not only has serious immediate effects (mortality), but long term population and demographic effects, such as local extirpation of colonies, reduced colony size, increased variance in local population sizes, and increased distances between colonies. The latter can reduce the effectiveness of dispersal among colonies to recolonize after local extinction and increase the probability of extinction for entire complexes (Culley and Williams 2001). The effects of plague on populations are even more devastating when coupled with shooting and poisoning. In fact the demographic changes imposed by such activities may place the species in an "extinction vortex" that *C. ludovicianus* may not recover from (Gilpin 1999). Populations west of the Dakotas commonly experience epizootics every 5-7 years (Culley, pers. comm.) and these outbreaks may hold the population level at about 40% of what it was before the epizootic (Knowles 1987).

In Wyoming plague continues to be a threat to black-tail populations. The disease has not yet expanded to cover the species national range, but nearly all Wyoming populations of white and black-tailed prairie dogs have witnessed declines due to plague outbreaks. Important locations of extensive black tailed colonies, such as Thunder Basin National Grassland, have experienced losses of up to 70% of the total active acreage due to plague epizootics (T. Byer, personal communication). The movement and maintenance of plague is not well understood (Anderson and Williams 1997) and needs further research. The occurrence of *Y. pestis* is generally west of the Dakotas. However, new reports indicate steady eastward movement in the southern part of the range, into Kansas (Cully et al. 2000).

Dispersal Capability

Cynomys ludovicianus are capable of dispersing from natal colonies as far as 5km; however, *C. ludovicianus* will rarely disperse beyond the natal colony due to predatory risk without the warning "predator" calls of conspecifics (see Dispersal). In fact, it is estimated that survival rate decreases by 40% for each 5km dispersal distance (Hof et al. 2002). Roach et al. (2001) showed that prairie dogs within a 264km^2 area of the Central Plains Experimental Range and Pawnee National Grasslands in northern Colorado had a dispersal rate among established colonies of about 39%. It is largely unknown how often *C. ludovicianus* disperse to previously unoccupied sites, but is thought to be rare. Garret and Franklin (1988) demonstrated that dispersal rates increased as available food resources decreased. In highly fragmented colonies (i.e., urban and agricultural development), dispersal capability may be limited. The inability to disperse may create areas of high population density, increased competition for resources, and result in decreased habitat quality, which may lead to population decline and increased inbreeding (see Johnson and Collinge 2004). Other factors that could affect the dispersal of *C. ludovicianus* is the availability of high-visibility corridors or attractants such as chirping of other prairie dogs (Hof et al. 2002).

Reproductive Capacity

Hoogland (2001) demonstrated that *C. ludovicianus* have lower intrinsic rates of increase and are consequently more vulnerable to colony extinction than most other rodents. Five factors are responsible for this slow reproduction: 1) survivorship is <60% in the first year, 2) only one litter/year is produced, even under optimal conditions, 3) only 6% of males copulate as yearlings, 4) the probability of weaning a litter each year is only 43%, and 5) mean litter size at first juvenile emergence is usually 3.08. In addition, females may breed in their first year, but generally do not breed until their second year. On top of that, free-ranging species may only live three – to four years (Hoogland 1995). As a result, *C. ludovicianus* are slow to recover from population crashes such as a plague epizootic and must rely on recolonization from other colonies to recover or reestablish (see Metapopulation Dyamics). Cincotta et al. (1987) suggest that dispersing prairie dogs do not reproduce during their first year in a new colony. This may also play a factor in reproductive capacity. In spite of these facts, some researchers have suggested that *C. ludovicianus* are capable of rapid population increases subsequent to substantial reductions (see USFWS 2004b).

Protected Areas

In some areas of the species range, prairie dogs are protected from anthropogenically induced effects on national monuments, wildlife refuges and specially protected areas of federally managed lands. One such area is a shooting restricted zone in Thunder Basin National Grassland, Wyoming which provides approximately 20,000 acres. However, in contrast to the species range as a whole, the amount of protected area present is a very small percentage. The lack of large tracts of protected prairie dog range has caused some concern among managers due to the inter-colony dispersal that must occur to ensure long term survival of colony complexes that necessarily span large areas of land. As conservation plans are formulated and adopted by various management agencies, the amount of protected area is expected to increase. However, the extent of protections afforded and the extent of land thus impacted is currently uncertain.

Population Viability Analyses (PVAs)

For purposes of intensive management a suitable PVA has not been developed (Luce 2001). However, an interactive, web-based PVA model has been completed by Michael Gilpin at San Diego State University (SDSU) and contracted with the USFWS is available to view and use at http://gemini.msu.montana.edu/ ~mgilpin.prairie_dog.html. This PVA gives an excellent overview of many aspects of prairie dog management including an introduction to the metapopulation structure of black-tails. The interactive "applets" allow the user to manipulate varying conditions that effect population size and persistence such as plague and shooting.

Conservation Action

Existing Conservation Plans

The eleven states within the range of *C. ludovicianus* began a multi-state conservation effort in 1998 to promote conservation and avoid the federal listing of *C. ludovicianus*. The Black-Tailed Conservation Assessment and Strategy (CA&S) was developed in 1999. The purpose of the CA&S is to manage, maintain, and enhance habitat and populations of *C. ludovicianus* across its historic range and reduce the number of threats impacting their viability through the cooperation of private, tribal, federal, and state landowners. It provides actions, opportunities, and incentives for interested parties to become involved with conservation efforts of *C. ludovicianus*, as well as management suggestions such as eliminating mandatory control, regulating seasons or possession limits, maintaining and conserving required habitat and ecosystems, and establishing core populations on public lands to provide animals for dispersal to uninhabited areas or individuals for recolonization (Van Pelt 1999). In 2003 a Multi-State Conservation Plan (MSCP) was completed as an addendum to the CA&S to provide guidelines under which adaptive management plans will be developed by individual states and their respective working groups representing all stakeholders viewpoints (see Luce 2003). Currently ten of the eleven states in the range of *C. ludovicianus* have developed or drafted state prairie dog management plans: Interagency Management Plan for Black-Tailed Prairie Dogs in Arizona (Van Pelt et al. 2001), Conservation Plan for Grassland Species in Colorado (CDOW 2003), Kansas Black-Tailed Prairie Dog Management Plan (Kansas Department of Wildlife and Parks 2002), A Species Conservation Plan for the Black- and White-Tailed Prairie Dogs in Montana (Knowles 1999), New Mexico, North Dakota, Oklahoma (see Luce 2003), South Dakota Black-tailed Prairie Dog Management Plan (Cooper and Gabriel 2005), Texas Black-Tailed Prairie Dog Conservation and Management Plan (TBTPDWG 2004), Draft Wyoming Black-Tailed Prairie Dog Management Plan (Kruckenberg et al. 2001; WBPDWG 2001). Together, the CA&S, the MSCP, and the eleven state management plans hope to remove enough threats to *C. ludovicianus* in order to curtail needs for listing under the ESA while allowing for more flexible management practices. The following target objectives were created in the MSCP to help achieve this goal:

1. Maintain at least the currently occupied acreage of black-tailed prairie dogs in the U.S. (see Table 1).
2. Increase to at least 1,693,695 acres of occupied black-tailed prairie dog acreage in the U.S. by 2011.

3. Maintain at least the current black-tailed prairie dog occupied acreage in the two complexes greater than 5,000 acres that now occur on the adjacent to Conata Basin-Buffalo Gap National Grassland, South Dakota, and Thunder Basin National Grassland, Wyoming.
4. Develop and maintain a minimum of 9 additional complexes greater than 5,000 acres (with each state managing or contributing to at least one complex greater than 5,000 acres) by 2011.
5. Maintain at least 10% of total occupied acreage in colonies or complexes greater than 1000 acres by 2011.
6. Maintain distribution over at least 75% of the counties in the historic range or at least 75% of the historic geographic distribution.

The issue of recreational shooting is slowly being addressed over much of the range of black-tailed prairie dogs. Licenses that were previously un-necessary to shoot *C. ludovicianus* are now required in all states except Montana and Wyoming. However new management ideas have been presented by the Wyoming citizen's working group. These ideas include: temporary closing of shooting if population numbers decline to 15% above objective (200,000 acres) from current levels, develop management units/licensing protocols, and work with the public to develop management strategies (WYGF 2001). In Wyoming, shooting restrictions were enacted on focal populations in Thunder Basin National Grassland during the spring of 2001 to allow populations to expand in anticipation of black-footed ferret reintroduction. Future yearlong closures are proposed by the Wyoming Game and Fish Department (WYGF) for areas considered as important focal regions for conservation of the species (WYGF 2001). Wyoming G&F has begun to develop a memorandum of understanding (MOU) between agricultural, weed and pest, and wildlife commissions to limit poison distribution and to develop land owner incentives for keeping prairie dogs on their lands (WYGF 2001).

The National Forest Service (NFS) has also adopted management strategies to conserve *C. ludovicianus* on NFS lands (i.e., Thunder Basin National Grassland, Dakota Prairie Grasslands, and Nebraska National Forest Land) which are occupied (>70%) by *C. ludovicianus* populations (USDA 2004). These strategies include guidance and directions for the use of rodenticides, landownership adjustment, vegetation management, livestock grazing, prairie dog shooting/hunting, and other management options to either expand or limit growth of prairie dog populations and colonies on NFS lands (see USFWS 2004c).

Conservation Elements

Although *C. ludovicianus* has not been listed as threatened or endangered by the Endangered Species Act, the long-term decline in abundance and distribution across its historic range suggests that there is a need to undertake conservation actions to mitigate such a decline while viable populations still exist. This need is compounded by the fact that the *C. ludovicianus* provides habitat and a food source for a variety of wildlife species, including the endangered black-footed ferret (see Community Ecology). In Wyoming, conservation efforts should be attentive, since far less habitat has been lost in Wyoming than in most other states within the species' distribution (WBTPDWG 2001) and only 79% of suitable habitat is currently occupied by *C. ludovicianus* in Wyoming (see Table 1). Five main conservation elements should be addressed for *C. ludovicianus* conservation management in Wyoming. For more rangewide suggestions, please review Van Pelt (1999). Specific approaches that have been proposed to address these conservation elements are provided in the following section.

1. **Habitat Conservation**: Reduce conversion of land to uses not compatible with local persistence of *C. ludovicianus* and minimize impacts of semi-compatible uses, including livestock grazing and resource extraction.
2. **Disease Control**: The spread of disease (specifically sylvatic plague) among *C. ludovicianus* should be investigated and management should seek to minimize its impacts on prairie dog complexes.

3. **Shooting and Extermination Control**: Unless strictly controlled, recreational shooting and pest control efforts aimed at killing *C. ludovicianus* are not compatible with healthy populations.
4. **Inventory and Monitor Populations**: Current monitoring efforts are insufficient to generate reliable and comparable trend information and are therefore inadequate to track the future of *C. ludovicianus* populations. A thorough and consistent methodology must be applied in Wyoming and across its range, as discussed in the Inventory and Monitoring section below.
5. **Public Education**: In order to apply the above mentioned conservation elements to successful management programs in Wyoming, public attitudes toward prairie dogs need to change. Literature citing the importance of *C. ludovicianus* to rangeland habitat and its associated species need to be easily acquired and come in a variety of materials (i.e., brochures, videos, information boards, etc.).

Acting on Conservation Elements

There are many state citizens' working groups that have developed or are currently drafting conservation plans for *C. ludovicianus* and provide suggestions for management practices for *C. ludovicianus*. In addition, research published that focused specifically on *C. ludovicianus* has also provided management suggestions that may provide the best opportunity to conserve preferred habitat and viable populations of *C. ludovicianus*.

1. **Habitat Conservation**: It appears that conservation efforts to protect lands currently occupied (and adjacent) by *C. ludovicianus* is beneficial for maintaining or increasing abundance (see Table 2). Identifying tracts of lands occupied by *C. ludovicianus* (especially those >5,000 acres; see Van Pelt 1999) should be conducted through coordinated efforts of all federal agencies to maximize the conservation potential and preserve, if not increase, occupied habitat. In Wyoming, this objective is no less than 200,000 acres (WBTPDWG 2001). Maintaining large tracts of land will provide enough acreage and *C. ludovicianus* population to support reintroduced and recovering black-footed ferret populations, as well as other associated species (Luce 2003). Lomolino et al. (2003) suggest a mixed strategy for preserving habitat: maintain or develop widely

distributed large and small complexes (connected for dispersal purposes; Roach et al. 2001), and retain small and large isolated colonies throughout the range to help create barriers to prevent spread of the plague and potential eradication of metapopulations. Create buffers (~75 feet) around protected areas to provide area for expansion. In cases where adjacent land is not compatible with prairie dog colonies (i.e., hay or crop fields), create barriers beyond the buffers (i.e., tall grasses) to prevent establishment and/or foraging in these sites (CBOS 1996). Provide incentives for private landowners to voluntarily maintain prairie dog colonies on portions of their lands, since conserving *C. ludovicianus* habitat is not fully possible without the assistance of private landowners. In Wyoming, this is important, since private land constitutes a large percentage of total prairie dog habitat (WBTPDWG 2001). The multi-state conservation plan outlines a possible incentive program that could be pursued by individual states under such authorities as the Conservation Title of the Farm bill, Conservation Reserve Program, or Grasslands Reserve Program in Appendix E (Luce 2003). In addition, impacts that could adversely affect established or potential *C. ludovicianus* through urban, oil, and/or gas development should be minimized or eliminated. The following are suggestions to mitigate habitat alteration:

- Identify suitable habitat and current colonies before proposed oil and gas exploration and urban development sites are initiated.
- Determine local population densities, quality of habitat, spatial distribution of colonies and habitats (for connectivity and dispersal purposes), and how activities (i.e., drilling) may impact these factors.
- Locate roads outside areas of current, recent, or potential prairie dog habitats identified.
- Place restrictions on vehicle traffic (for mining operations) during the breeding season and dispersal (March through August) to help minimize stress and possible increased infanticide.

2. **Disease Control**: Currently there are no known vaccines to immunize *C. ludovicianus* against threat of the plague. However, steps can be taken to mitigate plague impacts. The multi-state conservation plan (Appendix D; Luce 2003) provides a plague protocol for all eleven states to initiate. It includes a plague monitoring protocol, procedures for visual evaluation of prairie dog colonies for plague, field procedures for collecting and handling

carcasses as diagnostic specimens, and procedures for swabbing rodent burrows. It is important to identify colonies in which the plague affected populations, and try to isolate these colonies from other complexes to stop the spread of the disease. In this case, colonies should be greater than 3km from their nearest neighbor colonies (Cully and Williams 2001). In addition, implementing the suggested mixed-strategy complex design (connected complexes with isolated colonies) will help reduce disease transmission, while maintaining some vital corridors to facilitate repopulation of eradicated populations (see Lomolino et al. 2003).

3. **Shooting and Extermination Control**: Unless strictly controlled, recreational shooting may not be compatible with healthy populations of prairie dogs, altering behavior and reproductive success, especially if this activity increases (Reeve, personal communication; Vosburgh and Irby 1998; USFWS 2004b). Further, unlike some threats (e.g., disease) it is well under the control of land managers. Optimally, shooting should be eliminated, particularly on otherwise impacted towns (i.e., large plague epidemics). During the past few years, several states have established better regulations (i.e., closures and season restrictions) that allow for management of recreation shooting; as well, they have changed the status of species from pest to a designation that recognizes the need for management. However, inn Kansas, North Dakota, and Wyoming, *C. ludovicianus* is still considered a pest and controlled as such (Luce 2003). The following are some restrictions that could help regulate recreational shooting of *C. ludovicianus* to assist in the conservation and protection of the species (Luce 2003):
    - Seasonal closures to all shooting during whelping and dependent young period (March 1 to June 30).
    - Require permits specific to designated areas and limit take.
    - Collect data on harvest (i.e., age and sex of animals harvested), hunter days per county, and hunter days/harvested animal through annual field checks and mail surveys, allowing State Wildlife Agencies to accurately quantify annual harvest.

    In Wyoming, *C. ludovicianus* is considered a pest and management is overseen by the Wyoming Weed and Pest Council, Board of Agriculture, and Wyoming Game and Fish Commission. Currently a memorandum of understanding is being drafted in which these agencies agree to limit the distribution of poisons and their participation in poisoning efforts when survey results indicate conservation plan objectives (i.e., acreage) is in jeopardy. Temporary restrictions on agency poisoning or cooperation with landowners using poison or other control methods should be implemented at local levels when necessary (i.e., poisoning compounding impacts by other threats to populations; WBTPDWG 2001).

4. **Inventory and Monitor Populations**: Conducting a baseline, state wide inventory of the number of acres contained within is crucial for long term population monitoring of this species. This information will allow management agencies to develop population targets, identify important population centers throughout the state, and give a measurable level of increase or decrease in population size under new management regimes. Sidle et al. (2001) present new estimates of prairie dog abundance in four states that are critically important to conservation of *C. ludovicianus*, and present a new aerial survey technique for abundance estimation that is replicable, includes estimates of precision, and does not require trespass permission from private landowners (Miller and Culley 2001; Sidle et al. 2001). It is important that methods range-wide are compatible with each other for comparison. The following strategies were outlined in the Wyoming conservation plan (WBTPDWG 2001):
    - Develop a cooperative effort to fund and conduct research and regularly scheduled inventories.
    - Continue to develop remote census techniques (i.e., Sidle et al. 2001).
    - Evaluate aerial transect techniques to identify the approach and sampling design best suited for Wyoming (see Appendix IX).
    - Conduct selected techniques in areas where ground surveys are being conducted (e.g., Thunder Basin National Grasslands) and evaluate accuracy and precision of techniques.
    - Coordinate with adjacent states to assure that results will be comparable.
        - Select a reliable method, and initiate inventories to document occupied habitat (initiated July 2002).
        - Conduct monitoring survey at three-year intervals from 2002.
5. **Public Education**: Lamb et al. (2001) conducted an eleven state survey within short-grass prairie systems regarding the public's attitude and knowledge of black-tailed prairie dogs.

Overall, the public did not highly regard *C. ludovicianus* and did not consider conservation of *C. ludovicianus* of great importance when compared with larger environmental issues, such as global warming. People will only value grasslands and prairie dogs to the degree that they understand them. Therefore, education of prairie dog may increase the desire to manage prairie dogs, especially since the anti-prairie dog attitude is still pervasive in federal, state, and public views (Knowles 1999; Lamb et al. 2001). Education and outreach materials should cover many topics including but not limited to prairie dog management, prairie dog ecology, plague, and effects of prairie dogs on rangelands and agricultural land. It is important that outreach materials and education programs are factual and represent interests of all stakeholder groups (TBTPDWG 2004). Examples of educational techniques could be: in-school presentation, nature hikes, slide presentations, brochures, and interpretative displays (CBOS 1996).

Habitat Preservation and Restoration

Habitat fragmentation and transformation of the Great Plains grasslands biome has been the most extensive of any in North America. This habitat alteration has impacted the continuity of large, historic habitat needed to establish extensive networks of prairie dog colonies and maintain inter-colony genetic diversity. Clearly, this is an important component of future conservation efforts. Programs that create, protect, and restore suitable habitat and connectivity offer some promise to provide habitat for successful prairie dog colonies/populations.

Roe and Roe (2003) offer guidelines to be used when selecting habitat for *C. ludovicianus* relocation efforts, which could be used for habitat restoration/preservation efforts (see Table 3). The guidelines present environmental parameters specific to soils, vegetation height, cover, and palatable species, slope, and optimal proximity to other established prairie dog colonies. In addition, Lomolino and Smith (2003b) and Lomolino et al. (2003) recommend conserving a network of native prairie reserves strategically located across the historic range of *C. ludovicianus*. They suggest that the network be comprised of “clusters” of large (presumably >10 ha, but size is not directly specified by the authors) towns, as well as large, isolated towns. The latter will be less likely to be infected or serve as a source for spread of the plague. Large towns will also be more likely support populations of *C. ludovicianus* and other associated vertebrates into the future (Lomolino and Smith 2001), buffering adverse effects from various extrinsic extinction forces (i.e., land conversion, expansion of roads, habitat reduction and fragmentation, and plague).

When restoring habitat for reintroduction of *C. ludovicianus*, whether to provide a food-base for black-footed ferrets, or to reestablish *C. ludovicianus* in their historic range, long-term planning is needed, as well as sufficient 1) area of land and habitat, 2) pre-introduction ecological studies and site preparation, 3) breeding individuals to make a reproducing population, 4) protection, and 5) monitoring and follow up studies (AGFD 2004).

Information Needs

Identifying specific information needs will help management agencies to formulate appropriate conservation strategies by targeting key areas needed for effective conservation of the species. The following list briefly notes some of the key information needed to develop sound *C. ludovicianus* conservation strategies.

1. **Inventory/Monitoring**: The development of long term monitoring and inventory of black-tailed prairie dog populations is needed. Without a way to reliably and quantitatively determine trends in abundance and distribution, managers have no way to assess the status of *C. ludovicianus* populations or the effect of management actions on these populations. Inventories should determine locations and sizes of colonies, land ownership, and presence of plague. Monitoring of known *C. ludovicianus* populations will help managers assess the affects of impacts, such as oil and gas projects, on population trends. Remote sensing and aerial and ground techniques need to be developed and standardized among agencies to ensure validity, smooth information flow, and communication (see Sidle et al. 2001).

2. **Disease**: Plague continues as one of the most detrimental threats to this species longevity and healthy population growth. Although some research has investigated the dynamics of plague in prairie dog colonies, there are still huge questions regarding its prevalence, cycle of occurrence, and distribution in the natural environment. Managers need to know how plague spreads between colonies and how it is maintained within colonies. Strategies allowing managers to predict and mitigate epizootics is very important given the catastrophic impact this disease has had on prairie dogs; for instance, field trials of vaccinations or parasite management strategies and/or real-time, large-scale, high-resolution mapping of epidemics. It is unknown if prairie dogs may one day develop immunity to the disease or if virulence will stay high.
3. **Shooting and Poisoning**: Recreational shooting effects have been studied preliminarily (Knowles 1987, K. Gordon, pers. comm.), but further research is needed to fully understand the impact of this activity on demographic structure and population dynamics. Depending on the outcome of ongoing studies, shooting may continue in some areas, but regulation and monitoring of this activity are keys to controlling its effects as evidenced by many years of hunting regulation for game species.
4. **Ecological Ramifications**: More research is needed on the long-term effects of *C. ludovicianus* on floral, faunal, and soil communities to determine if they are indeed a keystone species, and important for the persistence of a variety of species (see Community Ecology above).

Tables and Figures

Table 1: Baily Eco-Region habitat model distributions for each state (Native American tribes in Montana, South Dakota, and North Dakota set acreage objectives independent of states.)

State	Historic Habitat*	Current Habitat	Gross Habitat**	Suitable Habitat***	Minimum 10-Yr Objective
AZ	7,047,137	0	7,047	4,594	4,594
CO	27,352,880	631,102	273,529	255,773	255,773
KS	35,835,079	130,521	150,714	148,596	148,596
MT	60,442,757	90,000	297,286	240,367[1]	240,367[1]
NE	36,035,433	80,000	146,741	137,254	137,254
ND	11,045,269	20,500	110,453	100,551[2]	100,551[2]
NM	39,021,449	60,000	96,661	87,132[3]	87,132[3]
OK	21,606,120	22,000	70,868	68,657	68,657
SD	29,262,553	160,000	218,121	199,472[4]	199,472[4]
TX	78,592,452	167,625	310,945	293,129	293,129
WY	22,067,599	125,000	179,072	158,170[5]	158,170[5]
Total:	368,308,727	1,486,748	1,861,436	1,693,695	1,693,695

* Refers to total potential habitat encompassed within the range (Hall 1981), not occupied habitat

** Gross habitat = total acreage of primary range x 1% + total acres of peripheral range x .1% (Table 2 and Figure 3)

*** Suitable habitat = gross habitat minus habitat with >10% slope, or other unsuitability factors (Agricultural lands were included in suitable habitat if they fit the slope and suitability factors)

1 The acreage objective in the State of Montana's 2001 Management Plan is 90,000-104,000 acres for non-tribal lands. The state's acreage objective will be subject to modification in response to a financial incentives program for landowners if an incentives program is funded. Separate objectives will be set by individual Native American tribes.

2 The current acreage objective listed in the North Dakota Management Plan is 33,000 acres, including non-tribal and tribal lands. The state of North Dakota and the Standing Rock Indian Reservation will determine the target acreage for each jurisdiction. The state is willing to consider an objective of 100,551 acres on non-tribal lands if a financial incentives program for private landowners is funded. Tribal lands will have separate acreage objectives.

3 The New Mexico acreage objective is based on a percent increase per year, which would take approximately 10 years to achieve the current acreage objective. If future statewide survey efforts indicate a different acreage than the estimated minimum current acreage listed, the rate for achievement of the 10-year objective will be adjusted accordingly.

4 The acreage objective for South Dakota includes 169,551 acres of non-tribal lands and 29,921 acres of tribal lands (pending final approval of management plan).

5 Wyoming's draft management plan contains an objective to maintain the current acreage, or 200,000 acres, which ever is greater.

Table 2: Overview of *C. ludovicianus* status throughout its range.

Country	State/Province	State Status (May 2004)	Heritage Rank	BLM Species of Concern	Population Trend (USFWS 2004b)
United States					
	Montana	Nongame Wildlife; Pest	S3	yes	Decreasing[3] Increasing/Stable[4,5]
	North Dakota	Nongame Wildlife	SU	yes	Stable?/Decreasing?
	South Dakota	Game Wildlife; Varmint	S4	yes	Increasing/Stable[4]
	Wyoming	Species of Special Concern	S2	yes	Decreasing[3] Stable[4]
	Nebraska	Nongame Wildlife	S4	nr	Absent[6] Increasing[4]
	Kansas	Wildlife	S3	nr	Absent[6] Increasing[4]
	Colorado	Small Game Species	S4	nr	Decreasing[1,3] Increasing[4,5]
	New Mexico	No Legal Listing	S2	no	Absent[6] Stable?
	Arizona	Extirpated; Nongame mammals	SX	no	Extirpated[1,2]
	Oklahoma	Species of Special Concern	S3	nr	Absent[6] Stable?
	Texas	Nongame Wildlife	S3	nr	?
Canada					
	Saskatchewan	Special Concern	S2	n/a	Stable[4]
Mexico					
	Amenazada	Threatened	n/a	n/a	Absent[1,2,6] Stable[4]

Heritage Rank: SU = unknown, SX = extirpated, S2 = imperiled, S3 = vulnerable, S4 = apparently secure

BLM Species of Concern:
yes = the State's BLM office recognizes *C. ludovicianus* as a Species of Concern
no = the State's BLM office does not recognize *C. ludovicianus* as a Species of Concern
nr = not reported

Population Trend: 1 = habitat conversion, 2 = control efforts, 3 = plague, 4 = habitat preservation, 5 = recovered, 6 = absent from historic range, ? = not enough information

Table 3: Guidelines for *C. ludovicianus* habitat restoration and preservation. Adapted from Roe and Roe (2003).

Parameters		**Description**
Vegetation	species	western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), sand dropseed (*Sporobolus cryptandrus*), cheatgrass (*Broums tectorum*), sixweeks fescue (*Vulpia octoflora*), ring myhly (*Muhlenbergia torreyi*), sedges (*Carex* spp.), scarlet globemallow (*Sphaeralcea coccinea*), and plains prickly pear (*Opuntia polyacantha*).
	cover	<40% bare ground; shortgrass prairie grasslands 58-70%; …
	height	<30cm
Soil	depth	≥2.0m
	type	loamy with little to no gravel; low in clay (<30%); meduim in sand (~50%); medium to high in silt (>70%) with good drainage.
Slope		< 20%; preferably ≤10%
Proximity to established colonies		≥46m and up to 185-277m

Figure 1: Photograph of adult and juvenile black-tailed prairie dog, Devils Tower National Monument, WY, © Steven W. Buskirk

Figure 2: Drawing of skull morphology of *C. ludovicianus*, adapted from Hoogland (1981).

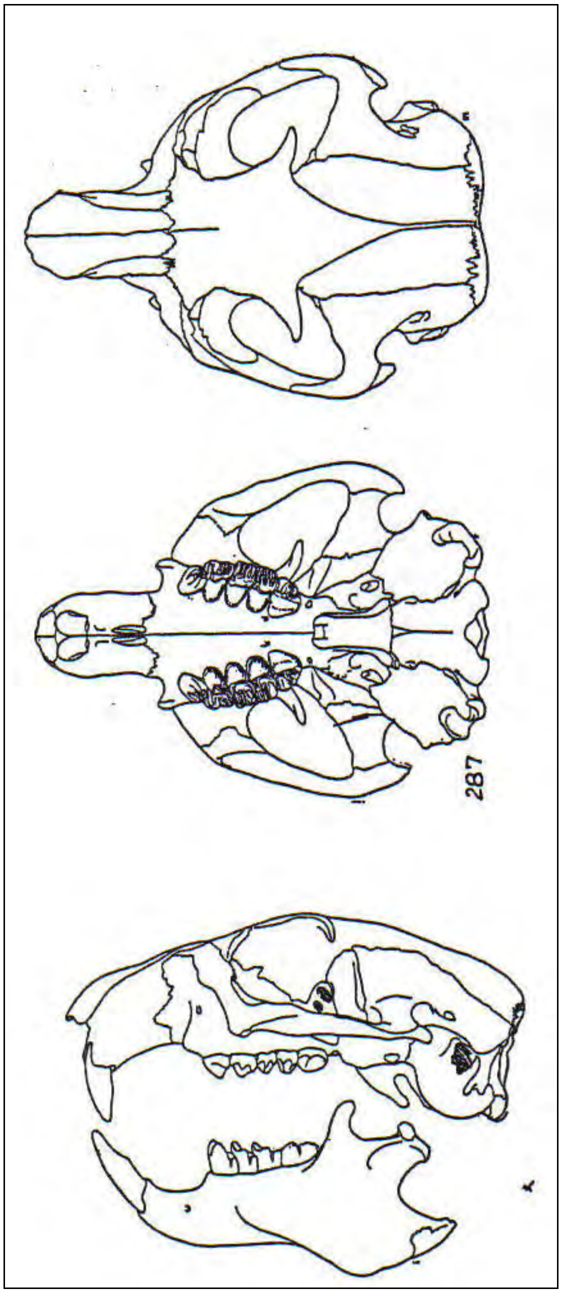
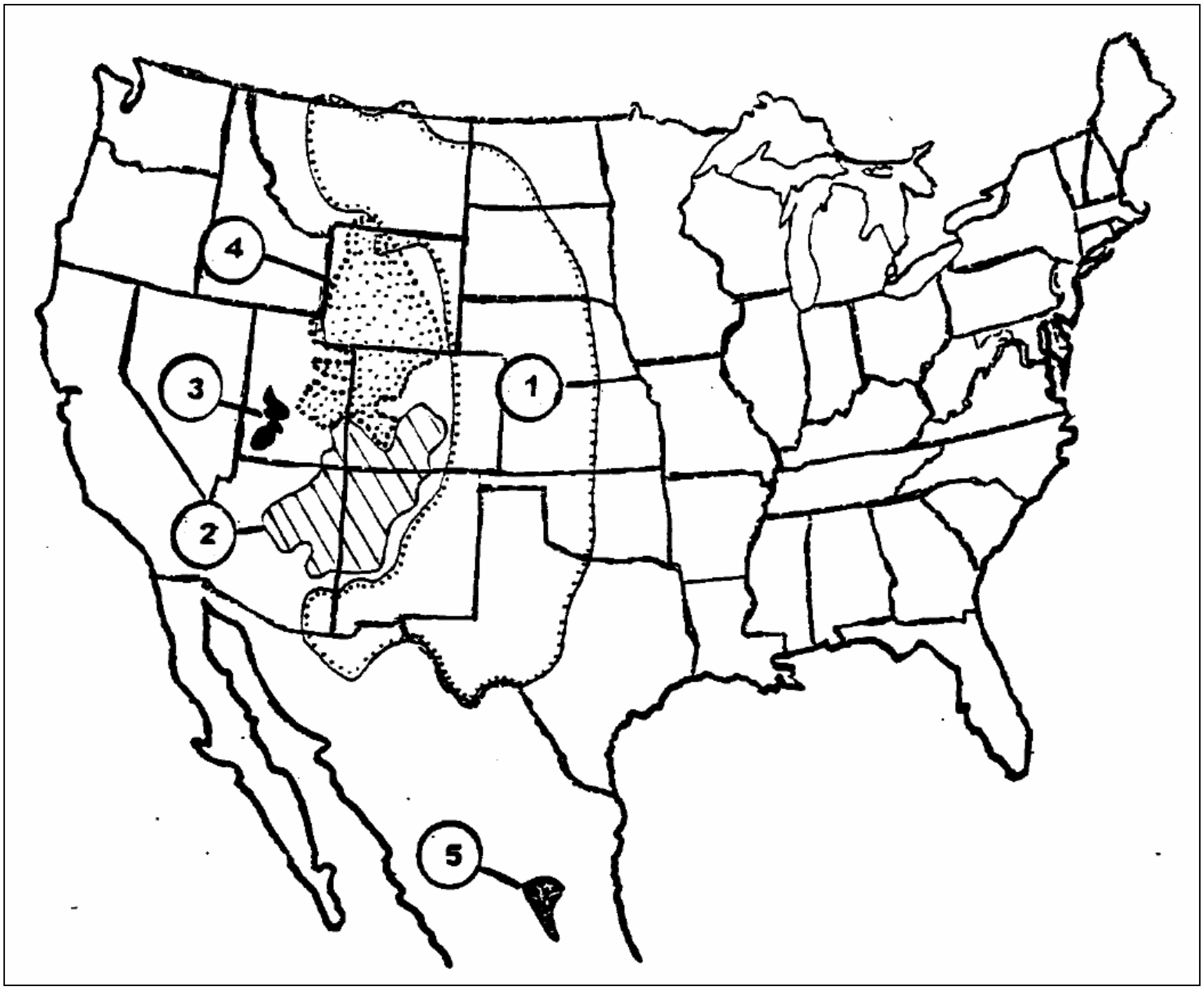


Figure 3: North American range of all prairie dog species from Hall (1981).



1. Black-tailed prairie dog
2. Gunnison's prairie dog
3. Utah prairie dog
4. White-tailed prairie dog
5. Mexican prairie dog

Figure 4: Possible distribution of *C. ludovicianus* based on mixed-grass and short-grass prairie distribution in eastern Wyoming (map acquired from WYGISC website: www.wygisc.uwyo.edu).

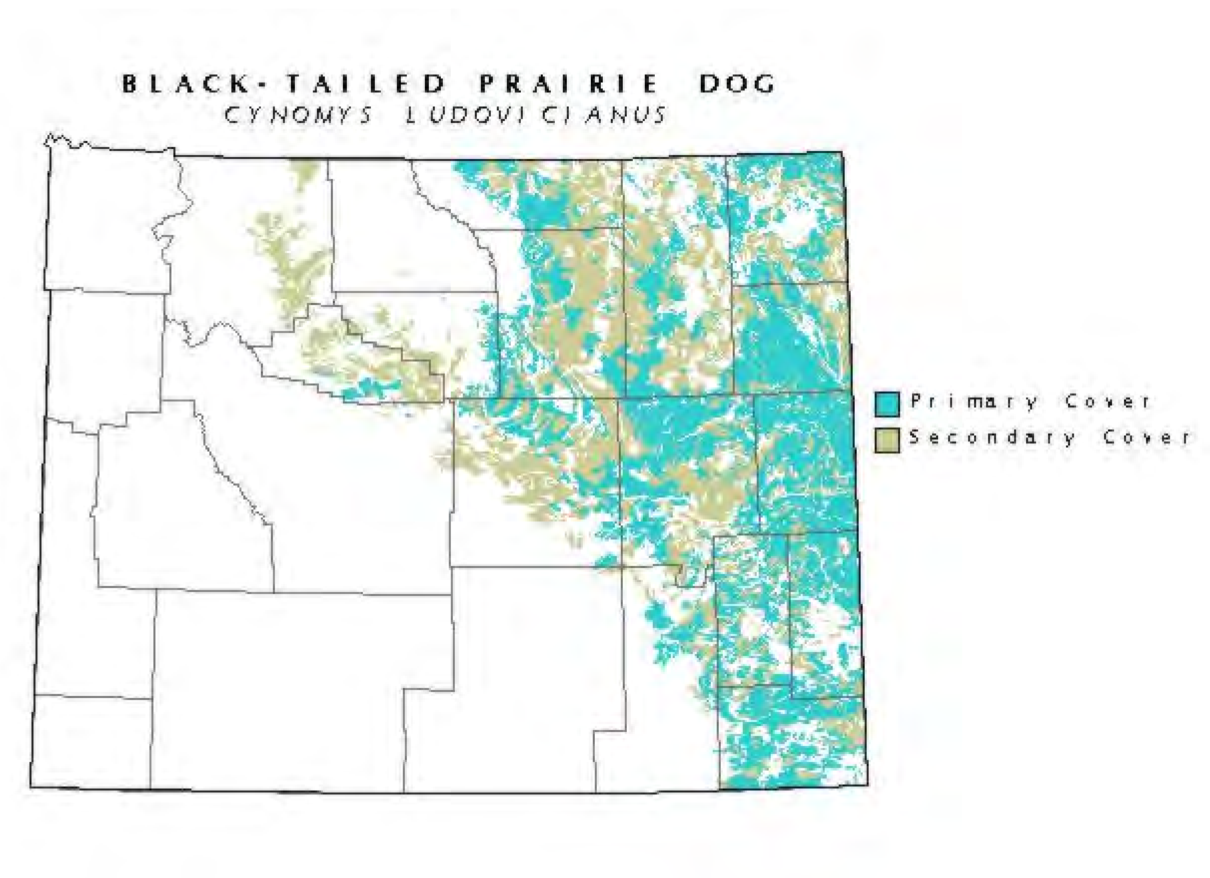


Figure 5: Rangewide distribution of the black-tailed prairie dog. Outline is the historic distribution from Hall (1981) and the shaded portion of the range map is from State surveys. This map does not include current distribution of populations in Canada and Mexico (acquired from Luce 2003).

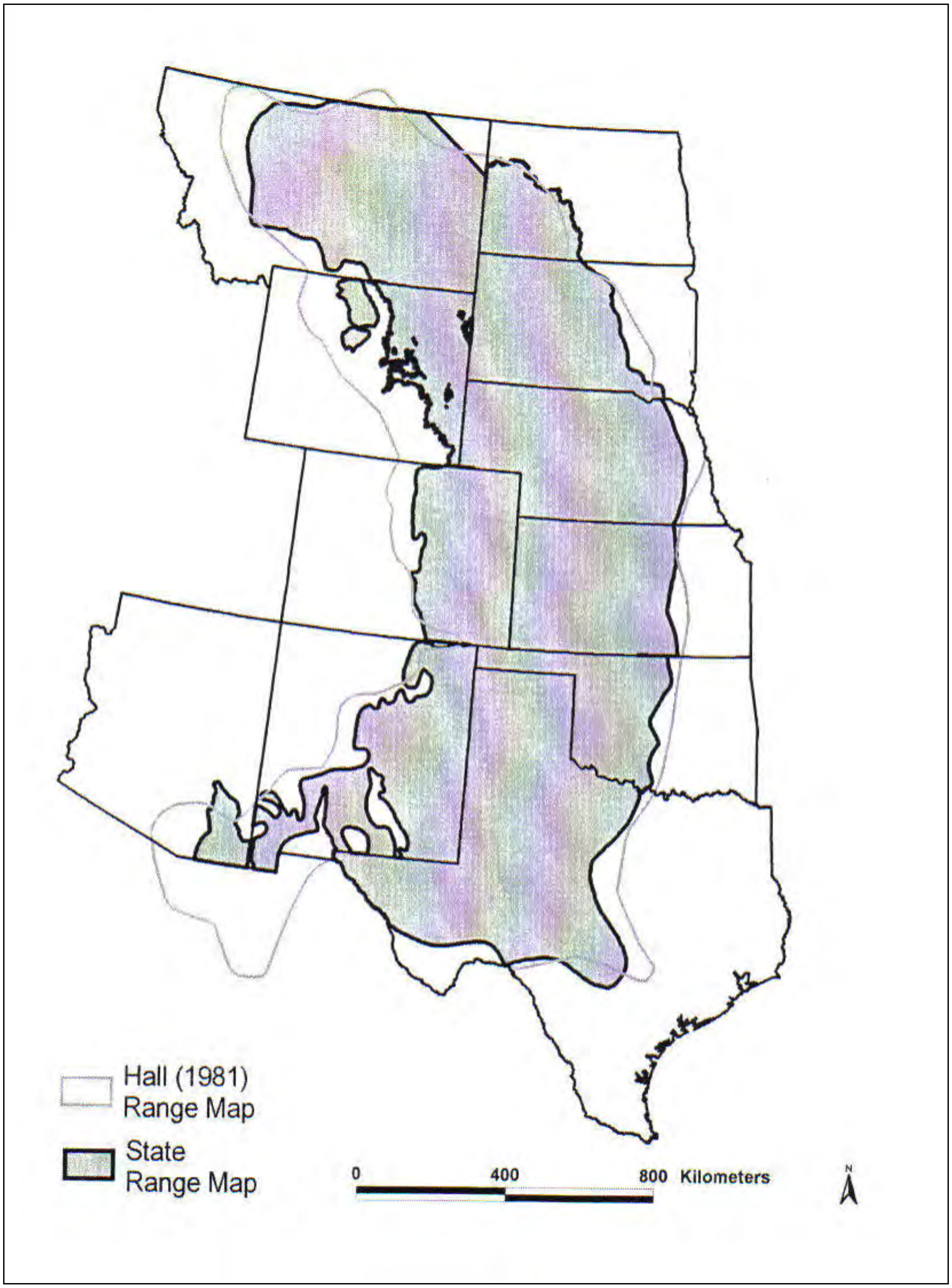


Figure 6. Loop diagram depicting a) life cycle and b) related matrix model elasticities for female black-tailed prairie dogs (*Cynomys ludovicianus*) (courtesy J. Pauli, University of Wyoming). Pi denotes the probability of surviving to the next age class and Fi denotes the fertility of that age class. eij denotes the elasticity from age class j to age class i. Although female black-tailed prairie dogs can reach an age of 9, age classes >6 were excluded in elasticity analyses because older age classes fail to reproduce. The basic loop diagram was constructed from J. Hoogland's 14 year study (1975-1988) of black-tailed prairie dogs in Wind Cave National Park (Hoogland 1995).

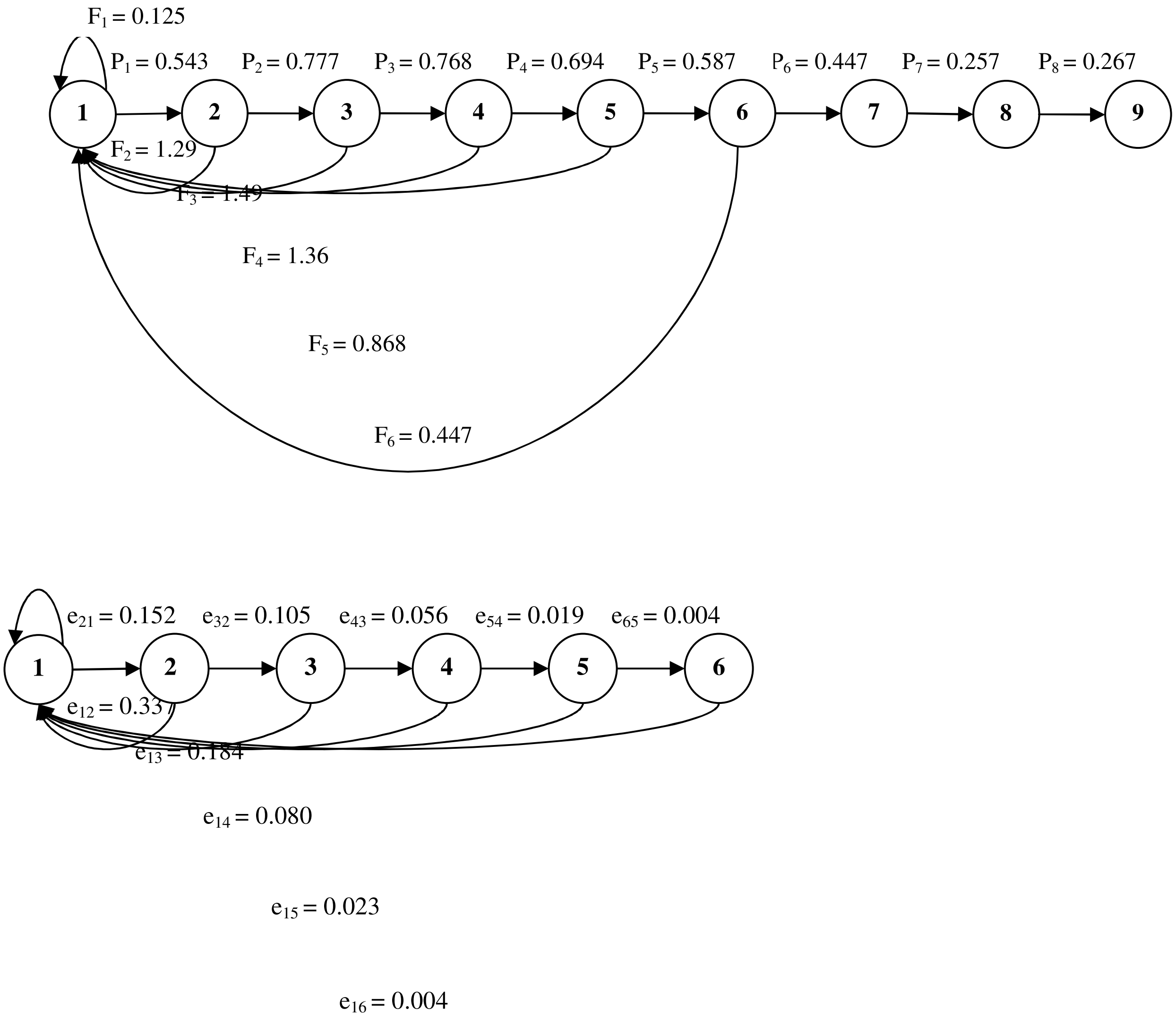


Figure 7: Map of Natural Heritage Ranks for the black-tailed prairie dog (NatureServe 2004).

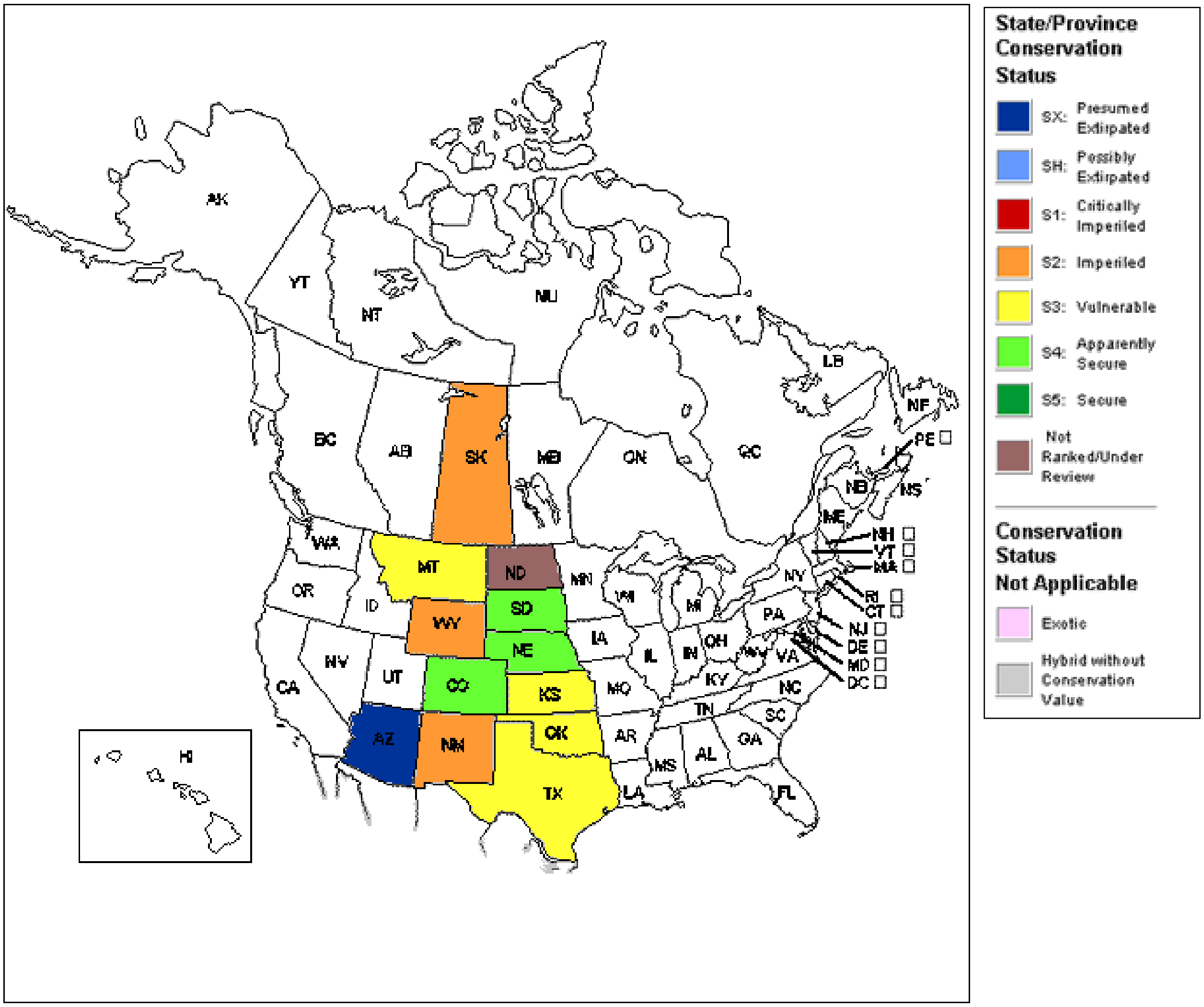
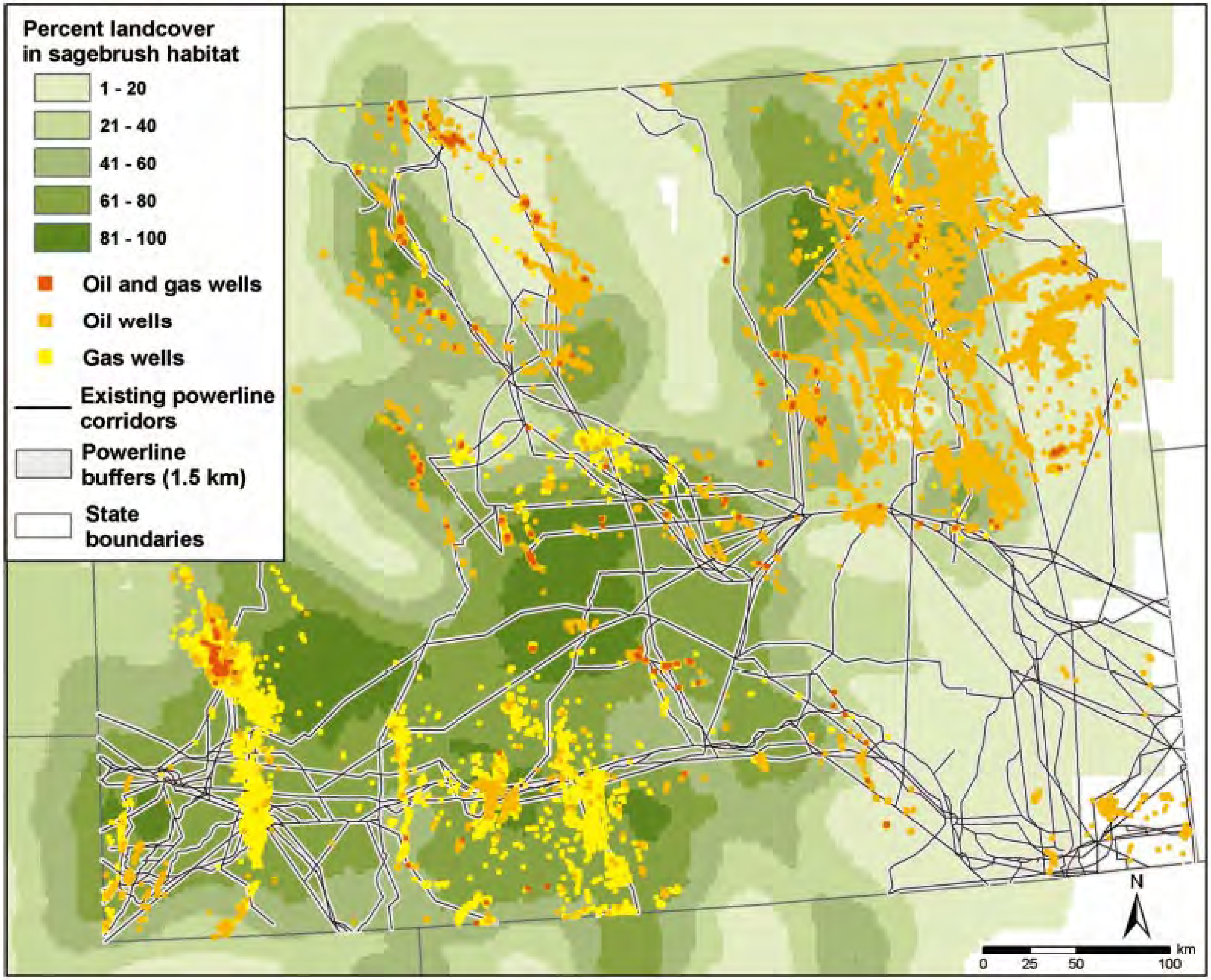


Figure 8: Existing oil and gas developments in Wyoming (Knick et al. 2003, p. 619). Note the amount of development in the northeast section of Wyoming, where the largest populations (acreage) of C. ludovicianus have been reported.



Literature Cited

Agnew, W., D. W. Uresk, and R. M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. Journal of Range Management **39**:135-139.

Agnew, W., D. W. Uresk, and R. M. Hansen. 1987. Arthropod consumption by small mammals on prairie dog colonies and adjacent ungrazed mixed grass prairie in western South Dakota. Pages 81-87 *in* Proceedings of the 8th Great Plains Wildlife Damage Control Workshop., Rapid City, SD.

Allan, P. F. and B. Osborn. 1954. Tall grass defeats prairie dogs. Soil Conservation **20**:103-105, 113.

Anderson, E., S. C. Forrest, T. W. Clark, and L. Richardson. 1986. Paleo-biology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes*, 1851. Great Basin Naturalist Memoirs. **8**:11-62.

Anderson, S. H. and E. S. Williams. 1997. Plague in a complex of white-tailed prairie dogs and associated small mammals in Wyoming. Journal of Wildlife Diseases **33**:720-732.

Anthony, A. and D. Foreman. 1951. Observations on the reproductive cycle of the black-tailed prarie dog (*Cynomys ludovicianus*). Physiological Zoology **24**:242-248.

Arizona Game and Fish Department (AGFD). 1988. Threatened native wildlife in Arizona. Arizona Game and Fish Department Publication. Phoenix, Arizona. 32 pp.

Arizona Game and Fish Department (AGFD). 2004. Unpublished abstract compiled and edited by the Heritage Data Management System, Arizona Game and Fish Department, Phoenix, AZ. 7pp.

Barko, V. A. 1996. Effect of the black-tailed prairie dog on avifaunal composition in southern shortgrass prairie. MS Thesis. Oklahoma State University, Stillwater, OK.

Becksted, M. 1977. Digestibility of common forage plants and energetic requirements of the black-tailed prairie dog. M.S. Thesis. South Dakota State University., Brookings.

Biggins, D. E., B. J. Miller, L. R. Hanebury, B. Oakleaf, A. H. Farmer, and R. Crete. 1993. A technique for evaluating black-footed ferret habitat.

Biggins, D. E., M. H. Schroeder, S. C. Forrest, and L. Richardson. 1985. Movements and habitat relations of radio-tagged black-footed ferrets. Pages 11.11-11.17 *in* S. H. Anderson and D. B. Inkley, editors. Black-footed ferret workshop proceedings. Wyoming Game and Fish Department, Laramie, Wyoming.

Biota Information System of New Mexico (BISON). 2004a. Black-tailed prairie dog (*Cynomys ludovicianus arizonensis*). New Mexico Department of Game and Fish and The Fish and Wildlife Information Exchange.

Biota Information System of New Mexico (BISON). 2004b. Black-tailed prairie dog (*Cynomys ludovicianus ludovicianus*). New Mexico Department of Game and Fish and The Fish and Wildlife Information Exchange.

Bonham, C. D., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. Journal of Range Management **29**:221-225.

Ceballos, G., J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Journal of Arid Environments **41**:161-172.

Cincotta, R.P., D.W. Uresk, and R.M. Hansen. 1987. Demography of black-tailed prairie dog populations re-occupying sites treated with rodenticide. Great Basin Naturalist. 47: 339-343.

City of Boulder Open Space Board of Trustees (CBOS). 1996. City of Boulder Grassland Management: Black-tailed Prairie Dog Habitat Conservation Plan. City of Boulder Open Space, Real Estate Department. 94pp.

Clark, T. W. and M.R. Stromberg. 1987. Mammals in Wyoming.

Clark, T.W., T.M. Campbell III, D.G. Socha, and D.E. Casey. 1982. Prairie dog colony attributes and associated vertebrate species. Great Basin Naturalist. 42: 572-582.

Clippinger, N. W. 1989. Habitat suitability index models: Black-tailed Prairie Dog. Biological Report 82, US Fish and Wildlife Service.

Collins, A. R., J. P. Workman, and D. W. Uresk. 1984. An economic analysis of black-tailed prairie dog (*Cynomys ludovicianus*) control. Journal of Range Management **37**:358-361.

Colorado Division of Wildlife (CDOW). 2003. Conservation plan for grassland species in Colorado. 205pp.

Cooper, J. and L. Gabriel. 2005. South Dakota black-tailed prairie dog conservation and management plan. South Dakota Department of Game and Fish and South Dakota Department of Agriculture. 76pp.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983a. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia **56**:1-9.

Coppock, D. L., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983b. Responses of bison to modification of vegetation by prairie dogs. Oecologia **56**:10-15.

Culley, J. F. 1989. Plague in prairie dog ecosystems: improtance for black-footed ferret management. *in* T. W. Clark, Hinckley, D. and Rich, T., editor. The prairie dog ecosystem: managing for biological diversity. MT Bureau of Land Management Wildlife Technical Bulletin #2.

Cully, Jr. J.F. and E.S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy. 82: 894-905.

Cully, J. F., A. M. Barnes, T. J. Quan, and G. Maupin. 1997. Dynamics of plague in a Gunnison's prairie dog colony complex from New Mexico. J Wildl Dis **33**:706-719.

Cully, J. F., L. G. Carter, and K. L. Gage. 2000. New records of sylvatic plague in Kansas. J Wildl Dis **36**:389-392.

Detling, J. K., and A. D. Whicker. 1987. Control of ecosystem processes by prairie dogs and other grassland herbivores. Pages 23-29 *in* Proceedings of the 8th Great Plains Wildlife Damage Control Workshop., Rapid City, SD.

Dinsmore, J. J. 1983. Mountain Plover (*Charadirius montanus*). Pages 185-196 *in* J. S. Armbruster, editor. Impacts of surface coal mining on 25 migratory birds of high federal interest. U.S. Fish and Wildlife Service.

Dobson, F.S., R.K. Chesser, J.L. Hoogland, D.W. Sugg, and D.W. Foltz. 2004. The influence of social breeding groups on effective population size in black-tailed prairie dogs. Journal of Mamamalogy. 85: 58-66.

Fagerstone, K. A., H. P. Tietjen, and O. Williams. 1981. Seasonal variation in the diet of black-tailed prairie dogs. Journal of Mammalogy **62**:820-824.

Feldhamer, G.A., L.C. Drickamer, S.H. Vessey, and J.F. Merritt. 2004. Mammalogy: Adaptation, Diversity, Ecology. Second Edition. McGraw Hill Higher Education, Boston, Massachusetts. 550pp.

Garret, M.G. and W.L. Franklin. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. Journal of Mammalogy. 69: 236-250.

Garrett, M.G., J.L. Hoogland, and W.L. Franklin. 1982. Demographic differences between an old and a new colony of black-tailed prairie dogs (*Cynomys ludovicianus*). American Midland Naturalist. 108: 51-59.

Gershman, M., project manager. 1996. City of Boulder Grassland Management: Black-tailed Prairie Dog Habitat Conservation Plan. Second edition. City of Boulder Open Space/ Real Estate Department. Boulder, Colorado. 94pp.

Gilpin, M. 1999. An Inquiry into the Population Viability of the Black-Tailed Prairie Dog. *in*. The National Fish and Wildlife Foundation.

Graul, W. D. 1980. Grassland management practices and bird communities. Pages 38-47 *in* Management of western forests and grasslands for nongame birds. U.S. Forest Service.

Hall, E. R. 1981. Mammals of North America. John Wiley and Sons, New York.

Hansson, L. 1971. Small rodent food, feeding and population dynamics. Oikos **22**:183-198.

Harlow, H. J., and G. E. Menkens. 1986. A comparison of hibernation in the black-tailed prairie dog, white-tailed prairie dog, and Wyoming ground squirrel. Canadian Journal of Zoology **64**:793-796.

Hof, J., M. Bevers, D.W. Uresk, G. L. Schenbeck. 2002. Optimizing habitat location for black-tailed prairie dogs in southwestern South Dakota. Ecological Monitoring. 147: 11-21.

Hoogland, J.L. 2001. Black-tailed, Gunnison's, and Utah prairie dogs reproduce slowly. Journal of Mammalogy. 82: 917-927.

Hoogland, J. L. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs. Ecology **63**:252-272.

Hoogland, J.L. 1982. Prairie dogs avoid extreme inbreeding. Science. 215: 1639-1641.

Hoogland, J. L. 1995. The Black-Tailed Prairie Dog: Social life of a Burrowing Mammal. The University of Chicago Press, Chicago, IL.

Hoogland, J. L. 1996. Mammalian Species No. 535 *Cynomys ludovicianus*. Journal of Mammalogy **535**:1-10.

Hoogland, J. L., D. K. Angell, J. G. Daley, and M. C. Radcliffe. 1987. Demography and population dynamics of prairie dogs. *in* Proceedings of the 8th Great Plains Wildlife Damage Control Workshop, Rapid City, SD.

Johnson, W.C. and S.K. Collinge. 2004. Landscape effects on black-tailed prairie dog colonies. Biological Conservation. 115: 487-497.

KDWP (Kansas Department of Wildlife and Parks). 2002. Kansas Black-tailed prairie dog management plan; final draft. Kansas Department of Wildlife and Parks, Laurence, Kansas.

Keinath, D.K. and G.P. Beauvais. 2003. Wyoming animal element ranking guidelines. Wyoming Natural Diversity Database, University of Wyoming, Laramie, Wyoming.

Keinath, D., B. Heidel, and G. Beauvais. 2003. Wyoming Plant and Animal Species of Concern. Prepared by Wyoming Natural Diversity Database. Laramie, Wyoming. 62pp.

Kelso, L. H. 1939. Food habits of prairie dogs. US Department of Agriculture Circular **529**:1-15.

Knick, S.T., D.S. Dobkin, J.T. Rotenberry, and M.A. Schroeder. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. The Condor. 105: 611-634.

Knight, D.H. 1994. Mountains and Plains: the Ecology of Wyoming Landscapes. Yale University Press. New Haven, Connecticut. 338pp.

Knowles, C. J. 1986. Some relationships of black-tailed prairie dogs to livestock grazing. Great Basin Naturalist **46**:198-203.

Knowles, C. J. 1987. An evaluation of shooting and habitat alteration of control of black-tailed prairie dogs. Pages 53-56 *in* Proceedings of the 8th Great Plains Wildlife Damage Control Workshop., Rapid City, SD.

Knowles, C.J. 1999. A species conservation plan for the black and white-tailed prairie dogs in Montana. Prepared for Montana Department of Fish, Wildlife, and Parks. Helena, Montana. 73pp.

Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs **3**:1-78.

Kruckenbert, L., R.Rothwell, and C. Burkett. 2001. Special report - draft Wyoming black-tailed prairie dog management plan. Wyoming Game and Fish Department. Cheyenne, Wyoming. 189pp.

Krueger, K. 1986. Feeding relationships among bison, pronghorn and prairie dogs: an experimental analysis. Ecology **67**:760-770.

Lamb, B.L., K. Cline, A. Brinson, N. Sexton, and P.D. Ponds. 2001. Citizen knowledge of and attitude toward black-tailed prairie dogs: completion report. Draft. U.S. Department of the Interior, U.S. Geological Survey. 61pp.

Lehmer, E.M., B. Van Horne, B. Kulbartz, and G.L. Florant. 2001. Facultative torpor in free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*). Journal of Mammalogy. 17: 103-128.

Lehmer, E.M., J.M. Bossenbrock, and B. VanHorne. 2003. The influence of environment, sex, and innate timing mechanisms on body temperature patterns of free-ranging black-tailed prairie dogs (*Cynomysludovicianus*). Physiological and Biotechnical Zoology. 76: 72-83.

Linner, S. 2001. Candidate and listing priority assignment form: black-tailed prairie dog (*Cynomys ludovicianus*). Region 6. 22pp.

Linner, S. 2002. Candidate and listing priority assignment form: black-tailed prairie dog (*Cynomys ludovicianus*). Region 6. 46pp.

Lomonlino, M.V. and G.A. Smith. 2001. Dynamic biogeography of prairie dog (*Cynomys ludovicianus*) towns near the edge of their range. Journal of Mammalogy. 82: 937-945.

Lomolino, M.V. and G.A. Smith. 2003a. Prairie dog towns as islands: applications of island biogeography and landscape ecology for conserving nonvolant terrestrial vertebrates. Global Ecology and Biogeography. 12: 275-286.

Lomolino, M.V. and G.A. Smith. 2003b. Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. Biological Conservation. 115: 89-100.

Lomolino, M.V., G.A. Smith, and V. Vidal. 2003. Long-term persistence of prairie dog towns: insights for designing networks of prairie reserves. Biological Conservation. 115: 111-120.

Luce, R.J. 2003. A multi-state conservation plan for the black-tailed prairie dog, *Cynomys ludovicianus*, in the United States - an addendum to the black-tailed prairie dog conservation assessment and strategy, November 3, 1999.

Luce, R. J. 2001. An umbrella, multi-state approach for the management of the black-tailed prairie dog, Cynomys ludovicianus, in the United States, an addendum to the black-tailed prairie dog conservation assessment and strategy, November 3, 1999. 79pp.

May, H.L. 2004. Black-tailed prairie dog (*Cynomus ludovicianus*). Fish and Wildlife Habitat Management Leaflet Number 23. Natural Resources Conservation Service, Wildlife Habitat Management Institute, Madison, Mississippi. 12pp.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology. 8: 667-681.

Miller, B. J., R. P. Reading, and S. Forrest. 1996. Prairie Night. Smithsonian Institution Press, Washington.

Miller, B. J., R. P. Reading, J. L. Hoogland, T. W. Clark, G. Ceballos, R. List, S. Forrest, L. Hanebury, P. Manzano, J. Pacheco, and D. W. Uresk. 2000. The role of prairie dogs as a keystone species: Response to Stapp. Conservation Biology **14**:318-321.

Miller, B., C. Wemmer, D. Biggins, and R. Reading. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. Environmental Management. 14: 763-769.

Miller, K.K. 2001. Wyoming Demographic and Economic Profile. Rural Policy Research Institute. 11pp.

Miller, S.D. and J.F. Cully, Jr. 2001. Conservation of black-tailed prairie dogs (*Cynomys ludovicianus*), Journal of Mammalogy. 82: 889-893.

Mulhern, D. W., and C. J. Knowles. 1995. Black-tailed prairie dog status and future conservation planning. Rocky Mountain Range and Experiment Station Technical Report. **RM-GTR-298**.

NatureSeve. 2004. *Cynomys ludovicianus* - black-tailed prairie dog. NatureServe Explorer: an online encyclopedia of life [web application]. Version 4.0. NatureServe, Arlington, Virginia. Available http://www.natureserve.org/exploreer. (Accessed: February 3 2005).

Oakleaf, B. A. Cerovski, and M. Grenier. 2002. Native species status matrix, March 2002. Appendix IV. *In* Threatened, endangered, and nongame bird and mammal investigations. A.O. Cerovski, editor. Wyoming Game and Fish Department, Cheyenne, Wyoming.

O'Melia, M. E., F. L. Knopf, and J. C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management **35**.

Reading, R. P. 1993. Toward an endangered species reintroduction paradigm: A case study of the black-footed ferret. Ph.D dissertation. Yale University, New Haven, CT.

Reading, R. P., and R. Matchett. 1997. Attributes of black-tailed prairie dog colonies in northcentral Montana. Journal of Wildlife Management **61**:664-673.

Roach, J.L., P. Stapp, B. Van Horne, and M.F. Antolin. 2001. Genetic structure of a metapopulation of black-tailed prairie dogs. Journal of Mammalogy. 82: 946-959.

Roe, K.A. and C.M. Roe. 2003. Habitat selection guidelines for black-tailed prairie dog relocations. Wildlife Society Bulletin. 31: 1246-1253.

Sharps, J. C., and D. W. Uresk. 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. Great Basin Naturalist **50**:339-345.

Sidle, J.G., D.H. Johnson, B.R. Euliss. 2001. Estimated aeral extent of black-tailed prairie dogs in the Northern Great Plains. Journal of Mammalogy. 82: 928-936.

Smith, R. E. 1967. The natural history of the prairie dog in Kansas. Museum of Natural History, University of Kansas **49**:1-39.

Stapp, P. 1998. A reevaluation of the role of prairie dogs in Great Plains Grasslands. Conservation Biology. 12: 1253-1259.

Sugg, D.W., R.K. Chesser, F.S. Dobson, and J.L. Hoogland. 1996. Population genetics meets behavioral ecology. Trends in Ecology and Evolution. 11: 338-342.

Summers, C. A., and R. L. Linder. 1978. Food habits of the black-tailed prairie dog in western South Dakota. Journal of Range Management **31**:134-136.

Texas Black-Tailed Prairie Dog Working Group (TBTPDWG). 2004. Texas black-tailed prairie dog conservation and management plan. Texas Parks and Wildlife Department. Publication PWD-BK-W7000-XXX (X/04). 54pp.

Tileston, J. V., and R. R. Lechleitner. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north central Colorado. American Midland Naturalist **75**:292-316.

Trudeau, K.M., H.B. Britten, and M. Restani. 2004. Sylvatic plague reduces genetic variability in black-tailed prairie dogs. Journal of Wildlife Diseases. 40: 205-211.

Tyler, J. D. 1968. Distribution and vertebrate associates of the black-tailed prairie dog in Oklahoma. PhD Dissertation. University of Oklahoma, Norman, Oklahoma.

Uresk, D. W. 1984. Black-tailed prairie dog food habits and forage relationships in western South Dakota. Journal of Range Management **37**:325-329.

Uresk, D. W., and A. J. Bjugstad. 1983. Prairie dogs as ecosystem regulators on the northern high plains. *in* Seventh North American Prairie Conference, Southwest Missouri State University, Springfield MO.

USDA. 2004. USDA Forest Service Update, September 2004: Black-tailed Prairie Dog Conservation. 1p.

USDOI BLM Wyoming. 2001. Sensitive species policy and list. Bureau of Land Management, Wyoming State Office, Cheyenne, Wyoming. Instruction memorandum no. WY-2001-040.

USFWS. 1999. 50 CFR Part 17: Endangered and Threatened Wildlife and Plants; 90-Day Finding for a Petition To List the Black-Tailed Prairie Dog as Threatened. Federal Register **64:14424-14428**.

USFWS. 2000. 50 CFR Part 17: Endangered and Threatened Wildlife and Plants; 12-Month Finding for a Petition To List the Black-Tailed Prairie Dog as Threatened. Federal Register **65: 5476-5488**.

USFWS. 2001. 50 CFR Part 17: Endangered and Threatened Wildlife and Plants; Candidate Assessment To List the Black-Tailed Prairie Dog as Threatened. Federal Register **66:54808**.

USFWS. 2002. 50 CFR Part 17: Endangered and Threatened Wildlife and Plants; Candidate Assessment To List the Black-Tailed Prairie Dog as Threatened. Federal Register **67:40657**.

USFWS. 2004a. 50 CFR Part 17: Endangered and Threatened Wildlife and Plants; 12-Month Finding for the Resubmitted Petition To List the Black-Tailed Prairie Dog as Threatened. Federal Register **69:24876**.

USFWS. 2004b. 50 CFR Part 17: Endangered and Threatened Wildlife and Plants; Finding for the Resubmitted Petition To List the Black-Tailed Prairie Dog as Threatened. Federal Register **69:51217-51226**.

USFWS. 2004c. Black-tailed Prairie Dog Conservation and Management on the Nebraska National Forest and Associated Units. Federal Register. 69: 63350-63352.

Van Pelt, W.E. 1999. The black-tailed prairie dog conservation assessment and strategy. Nongame and Endangered Wildlife Program Technical Report 159. Arizona Game and Fish Department, Phoenix, Arizona.

Van Pelt, W.E., A. Averill-Murray, and T.K. Snow. 2001. Interagency Management Plan for Black-tailed Prairie Dogs in Arizona. Arizona Game and Fish Department.

VanPutten, M., and S. D. Miller. 1999. Prairie dogs: the case for listing. Wildlife Society Bulletin **27**:1110-1120.

Vosburgh, T.C. and L.R. Irby. 1998. Effects of recreational shooting on prairie dog colonies. The Journal of Wildlife Management. 62: 363-372.

Weltzin, J. F., S. Archer, and R. K. Heitschmidt. 1997a. Small mammal regulation of vegetation structure in a temperate savanna. Ecology **78**:751-763.

Weltzin, J. F., S. L. Dowhower, and R. K. Heitschmidt. 1997b. Prairie dog effects on plant community structure in southern mixed grass prairie. The Southwestern Naturalist **42**:251-258.

Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. Bioscience **38**:778-785.

Wuerthner, G. 1997. Viewpoint: the black-tailed prairie dog - headed for extinction? Journal of Range Management. 50(5): 459-466.

Wydeven, P. R., and R. B. Dahlgren. 1982. A comparison of prairie dog stomach contents and feces using a microhistological technique. Journal of Wildlife Management **46**:1104-1106.

WYGF. 2001. Wyoming black-tailed prairie dog management plan and conservation efforts. Wyoming Game and Fish Department, Cheyenne, WY.

Wyoming Black-Tailed Prairie Dog Working Group (WBPD Group). 2001. Draft Wyoming Black-tailed Prairie Dog Management Plan. 61pp.

Additional References

Baker, B.W., T.R. Stanley, and G.E. Plumb. 2000. Nest predation on black-tailed prairie dog colonies. Journal of Wildlife Management. 64: 776-784.

Barko, V.A., M.W. Palmer, J.G. Stewart, and D.M. Engle. 2001. Vascular plant communities associated with black-tailed prairie dog colonies in southern shortgrass prairie. Proceedings Okla. Acad. Sci. 81: 11-19.

Belak, J.R. 2001. Modeling the effects of habitat quality on black-tailed prairie dog habitat occupancy using spatially correlated data. Master's thesis. Colorado State University, Ft. Collins, Colorado. 127pp.

Desmond, M. 2004. Effects of grazing practices and fossorial rodents on a winter avian community in Chihuahua, Mexico. Biological Conservation. 116: 235-242.

Hoffman, B. 2000. Black-tailed prairie dog study of eastern Colorado. EDAW, Inc. Ft. Collins, Colorado. Prepared for Colorado Department of Natural Resources. 49pp.

Hoogland, J.L. 2003. Sexual dimorphism of prairie dogs. Journal of Mammalogy. 84: 1254-1266.

Hosch, T.L. 1999. The effects of fasting and appetite on body weight regulation and the induction of torpor in white-tailed and black-tailed prairie dogs. Master's Thesis. University of Wyoming, Laramie, Wyoming. 103pp.

InfoNatura: Birds, mammals, and amphibians of Latin America [web application]. 2004. Version 3.2. Arlington, Virginia (USA): NatureServe. Available: http://www.natureserve.org/infonatura. (Accessed: February 3, 2005).

Lamb, B.L. and K. Cline. 2003. Public knowledge and perceptions of black-tailed prairie dogs. Human Dimensions of Wildlife. 8: 127-143.

Lehmer, E.M. and B. Van Horne. 2001. Seasonal changes in lipids, diet, and body composition of free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*). Canadian Journal of Zoology. 79: 955-965.

Licht, D.S. and K.D. Sanchez. 1993. Association of black-tailed prairie dog colonies with cattle point attractants in the northern Great Plains. Great Basin Naturalist. 53: 385-389.

Reading, R. P., and S. R. Kellert. 1993. Attitudes toward a proposed reintroduction of black-footed ferrets (*Mustela nigripes*). Conservation Biology **7**:569-580.

Sidle, J. and M. Bosch. 2004. USDA Forest Service Update: Black-tailed prairie dog conservation. United States Forest Service.

Smith, G.A. and M.V. Lomolino. 2004. Black-tailed prairie dogs and the structure of avian communities on the shortgrass plains. Oecologia. 138: 592-602.

Vermeire, L.T., R.K. Heitschmidt, P.S. Johnson, and B.F. Sowell. 2004. The prairie dog story: do we have it right? BioScience. 54: 689-695.

Willey, S. 2004. Species assessment and listing priority assignment form: black-tailed prairie dog (*Cynomus ludovicianus*). 48pp.

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associated with food analysis in gizzards of blue-winged teal. J. Wildl. Manage. 34:739–746.
THOMPSON, D. 1973. Feeding ecology of diving ducks on Keokuk Pool, Mississippi River. J. Wildl. Manage. 37:367–381.
WILSON, E. S. 1922. An enormous flock of canvas-backs (*Marila valisineria*) visit the Detroit River. Auk 39:250–251.

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ALTERATION OF BISON AND BLACK-TAILED PRAIRIE DOG GRAZING INTERACTION BY PRESCRIBED BURNING

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Abstract: Bison (*Bison bison*) use of a black-tailed prairie dog (*Cynomys ludovicianus*) colony was compared before and after a prescribed burn on adjacent, uncolonized grassland at Wind Cave National Park (WCNP), South Dakota, 1979–80. On a daily basis cow-calf herds increased their use of the burned grassland 12× and decreased their use of the colony by 30–63% following the burn. Prescribed burns could be effective in mitigating bison impacts on colonies.

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Bison are attracted to grassland sites altered by prairie dogs (Koford 1958, McHugh 1958, Shult 1972). Coppock et al. (1983*a*,*b*) demonstrated that bison feed selectively on moderately grazed, grass-dominated areas near the perimeters of prairie dog colonies. These areas have more readily digestible perennial grasses with higher nitrogen concentrations and greater accessibility of green tissues than vegetation from uncolonized areas (Coppock et al. 1983*a*). Prairie dog colonies may receive a disproportionate amount of bison use in relation to their area. For example, a colony that comprised 39% of Pringle Valley in WCNP, South Dakota, received 90% of all bison feeding activity in that valley during the summer of 1979 (Coppock et al. 1983*b*).

Prolonged grazing pressure on colonies results in marked changes in plant composition (Coppock et al. 1983*a*), and because bison exacerbate impacts of prairie dogs (Coppock et al. 1983*b*), ways are needed to attract bison elsewhere. Because ungulates are attracted to burns (Vogl and Beck 1970, Davis 1977), we hypothesized that bison use of burned areas would increase with an accompanying reduction of their preferential use of prairie dog colonies. The objectives of this study were to contrast feeding-site selection by bison before and after a prescribed burn of grassland adjacent to a prairie dog colony and to evaluate the implications for management at WCNP.

We thank R. W. Klukas and the WCNP staff for facilitating our research. We gratefully appreciate the logistical assistance of Drs. J. H. Bock and C. E. Bock (Dep. Environ. Popul., and Organ. Biol., Univ. Colorado, Boulder), and the help of T. B. Fraas, B. D. Gueck, and P. I. Schiefer during data collection. This work was supported by Natl. Sci. Found. grants DEB-7682821 and BSR-8406660.

METHODS

Studies were conducted in Pringle Valley (120 ha) in the northwest corner of WCNP. The uncolonized grassland (84 ha) was dominated by little bluestem (*Andropogon scoparius*), big bluestem (*A. gerardi*), Kentucky bluegrass (*Poa pratensis*), and western wheatgrass (*Agropyron smithii*). The prairie dog colony (36 ha) contained plant associations that ranged from closely cropped grass-dominated areas (27 ha) in the outer margins to a forb (sweetclover [*Melilotus* spp.], ragweed [*Ambrosia*], and aster [*Aster* spp.]) and dwarf-shrub (fringed sagebrush [*Artemisia frigida*]) community (9 ha) in the center.

A 9-ha prescribed burn was conducted on

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Table 1. Percent availability and average relative feeding use of various sites by bison in Pringle Valley, Wind Cave National Park, South Dakota, during the summers (Jun–Aug) of 1979 and 1980. Feeding index values >1.0, 1.0, and <1.0 indicate selection, random use, and avoidance, respectively. Entries in the same column accompanied by the same letter denote significant differences ($P < 0.05$) in feeding-site selectivity either within a herd type between years (A) or between herd types within years (B).

	Site					Sampling	
Category	Off-colony[a] unburned	Off-colony burned	Young colony (grass-dominated)	Old colony (forb and dwarf-shrub dominated)	Daily use ranking (P)[b]	Days (N)	$\bar{x}$ daily feeding time (animal hours)
Availability (%)	50	11	28	11			
Feeding indices							
Cow-calf herds							
Preburn (1979)	0.19	0.20 A	2.79 A	0.92 A	<0.01	8	225
Postburn (1980)	0.29 B	2.46 AB	1.95 A	0.34 A	<0.01	19	289
Bull groups							
Preburn (1979)	0.10 A	1.51	2.09	1.92 A	>0.05	14	13
Postburn (1980)	0.56 AB	1.02 B	2.04	0.46 A	<0.01	35	24

[a] Colony denotes black-tailed prairie dog colony.

[b] Significance denotes high daily repeatability of pattern as evaluated using Friedman's test (Steel and Torrie 1980:546).

uncolonized grassland adjacent to the northeast edge of the colony in October 1979. The burn resulted in extensive reductions of standing-dead grass and litter (Bock and Bock 1983, 1984).

Observers quantified bison site selection and behavior (feeding or resting) from June to August in 1979 (preburn) and 1980 (postburn) from a fire tower. Bison location and site-specific activity during the daylight hours were recorded at 30-minute intervals (Coppock et al. 1983*b*). Observations were made daily in 1980 but only 5 days/week in 1979. Valley sites included: (1) the grass-dominated (young) portion of the colony (28% of the area as visible from the tower), (2) the old forb and dwarf-shrub area of the colony (11%), (3) the uncolonized grassland before and after burning (11%), and (4) unburned, uncolonized grassland (50%). Bison feeding-site selectivity was calculated daily for cow-calf herds (typically >100 animals) and bull groups (typically ≤5 animals). Cows with young were transient visitors to the valley, whereas bulls were present throughout the summer. Feeding-site selectivity was calculated as the percent observed : percent expected feeding time for a given site. Expected percentage of feeding time was assumed to be equal to the percent availability of sites if feeding was random. Random use would yield an index of 1.0 for all sites, whereas selection or avoidance of areas would yield values greater or less than 1.0, respectively.

Each day of observation was considered an independent sample of bison use of the valley. Friedman's test (Steel and Torrie 1980:546) was used to evaluate the daily repeatability of feeding pattern for cow-calf herds and bull groups in each year by ranking the site-selection indices (Coppock et al. 1983*b*). Because this index was distributed normally, *t*-tests were used to compare mean selectivity values for each site between bison herd types in each year and between years for each herd type.

RESULTS

Approximately 8,300 animal hours of feeding time were recorded during 76 days across both years. About 70% of the observations occurred in 1980 (Table 1). Although we did not keep a daily census for bulls in 1979, daily records indicate cow-calf herds increased their use of the valley in 1980 (21 total visits, of which 19 were sampled) compared to 1979 (16 total visits, of which 8 were sampled).

Before the burn in 1979, cow-calf herds grazed nearly 3× as much as expected on the young colony site, randomly used the old colony, and used the uncolonized areas less than expected in a highly repeatable daily pattern (Table 1). Site selectivity by bull groups was similar to this, but bulls were more variable on a daily basis. Following the burn in 1980, cow-calf herds exhibited a 12× increase ($P < 0.01$) in selection for the burned site, and significantly reduced ($P < 0.05$) their selection for the young and old colony for feeding compared

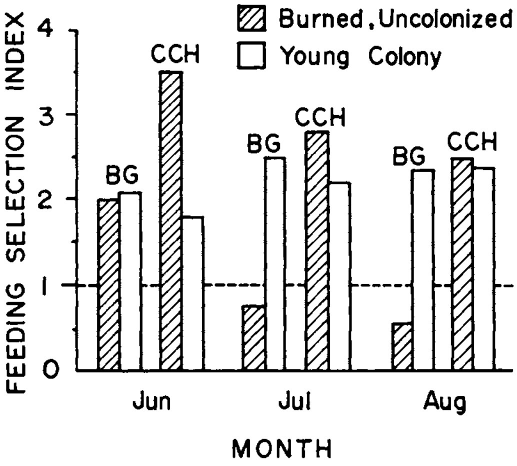

Fig. 1. Monthly feeding selection of a burned, uncolonized site and a young, grass-dominated black-tailed prairie dog colony site by bison in Pringle Valley, Wind Cave National Park, South Dakota, 1980. The selection index was calculated as percent total feeding use divided by percent site availability; values >1.0, 1.0, and <1.0 indicate selection, random use, and avoidance, respectively. BG = bull groups and CCH = cow-calf herds.

with the previous year (Table 1). In contrast, the burn had little effect on use of the valley by bull groups. The burn site and young colony were selected to a similar degree ($P > 0.05$) by bulls in both years, yet significant ($P < 0.01$) changes in selection of old colony and other off-colony areas occurred between years (Table 1).

Monthly patterns of feeding-site selection also varied between cow-calf herds and bull groups in 1980. The most pronounced variation occurred for selection of the burned site, as use of the young colony was consistently high by all bison throughout the summer (Fig. 1). Although all bison groups selected the burned site more in June, bulls used it less than expected in July and August. In contrast, cow-calf herds exhibited a high selection for the burned site regardless of month (Fig. 1).

DISCUSSION

Our results indicated that cow-calf herds did increase their use of the burned site the 2nd year and consequently decreased their use of the prairie dog colony for feeding. Bison may have been attracted to the burn because of chemical and structural changes in the vegetation that produced a higher diet quality for animals grazing there. Burning has been demonstrated to enhance forage nutrient content (Campbell et al. 1954, Bendell 1974, Hobbs and Spowart 1984), but effects may be minor and short-lived unless followed by frequent regrazing. Hobbs and Spowart (1984) suggested that increased accessibility of green forage was the major factor in the higher diet quality of montane ungulates using burned sites. This is a particularly good hypothesis for bison, which are relatively unselective feeders and may otherwise ingest large proportions of standing-dead herbage along with live tissue from stands of mature grasses.

Bulls were less attracted to the burned site than cow-calf herds. This might be explained by large differences in group size, which may have influenced the perception of, or need to exploit, so large a feeding patch. Both cow-calf herd and bull groups tended to use the burned site more in June before extensive greenup of Pringle Valley, which was dominated by warm season grasses. However, only cow-calf herds consistently regrazed the burned site during the rest of the summer. It is possible that bulls could better satisfy their foraging needs from a greater array of smaller patches. The regular use of the colony (also a large patch) by bulls appears contradictory to this argument, but this area, unlike the burned site, had the additional attraction of wallows (Coppock et al. 1983*b*). Dusting activities by bulls usually intensify by mid-summer because they are associated with antagonistic activities among males during the rut (Petersburg 1973). Wallowing, as well as better foraging conditions, may have contributed to the attraction of the colony for bulls. Such activity complicates comparisons of site selection based on forage characteristics alone.

Because cow-calf herds comprise nearly 70% of the bison in WCNP, the observation that burning can lure them from prairie dog colonies is important for grazing and habitat management. Heavy grazing by bison likely contributes to long-term changes in plant composition and productivity on colonies and may hinder vegetative recovery in sites where prairie dog populations have been reduced to meet management objectives. This study indicates that use of the colony by cow-calf herds for grazing was reduced about 35%/visit in postburn 1980 compared with preburn 1979. However, this daily reduction may have been largely negated by the increased use of this valley during the 2nd year, and the increased use may have been causally related to the prescribed burn. Therefore, we recommend that burning be located a considerable distance from colonies to minimize bison impacts. Control burning has been suggested as a useful tactic in manipulating free-ranging herds (Edwards 1984), and it may be possible to include this perspective within the ongoing management program at WCNP. Strategic placement of burns also should incorporate knowledge of bison travel routes and distributions of mineral licks and water.

LITERATURE CITED

BENDELL, J. F. 1974. Effects of fire on birds and mammals. Pages 73–138 *in* T. T. Kozlowski and C. E. Ahlgren, eds. Fire and ecosystems. Academic Press, New York, N.Y.

BOCK, C. E., AND J. H. BOCK. 1983. Responses of birds and deer mice to prescribed burning in ponderosa pine. J. Wildl. Manage. 47:836–840.

BOCK, J. H., AND C. E. BOCK. 1984. Effect of fires on woody vegetation in the pine-grassland ecotone of the southern Black Hills. Am. Midl. Nat. 112:35–42.

CAMPBELL, R. S., E. A. EPPS, C. C. MORELAND, J. L. FARR, AND F. BONNER. 1954. Nutritive value of native plants on forest range in central Louisiana. La. Agric. Exp. Stn. Bull. 488. 18pp.

COPPOCK, D. L., J. K. DETLING, J. E. ELLIS, AND M. I. DYER. 1983*a*. Plant-herbivore interactions in a North American mixed-grass prairie I. Effects of black-tailed prairie dogs on interseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56: 1–9.

———, J. E. ELLIS, J. K. DETLING, AND M. I. DYER. 1983*b*. Plant-herbivore interactions in a North American mixed-grass prairie II. Responses of bison to modification of vegetation by prairie dogs. Oecologia 56:10–15.

DAVIS, P. R. 1977. Cervid response to forest fire and clearcutting in southeastern Wyoming. J. Wildl. Manage. 41:785–788.

EDWARDS, P. J. 1984. The use of fire as a management tool. Pages 349–362 *in* P. de V. Booysen and N. M. Tainton, eds. Ecological effects of fire in South African ecosystems. Springer-Verlag, Berlin, W. Ger.

HOBBS, N. T., AND R. A. SPOWART. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. J. Wildl. Manage. 48:551–560.

KOFORD, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildl. Monogr. 3. 78pp.

MCHUGH, T. 1958. Social behavior of the American buffalo (*Bison bison bison*). Zoologica 43:1–40.

PETERSBURG, S. A. 1973. Bull bison behavior at Wind Cave National Park. M.S. Thesis, Iowa State Univ., Ames. 302pp.

SHULT, M. J. 1972. American bison behavior patterns at Wind Cave National Park. Ph.D. Thesis, Iowa State Univ., Ames. 178pp.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics. 2nd ed. McGraw-Hill Book Co., New York, N.Y. 633pp.

VOGL, R. J., AND A. M. BECK. 1970. Responses of white-tailed deer to a Wisconsin wildfire. Am. Midl. Nat. 84:270–273.

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DEFENDERS OF WILDLIFE
PRAIRIE DOG COALITION
THE HUMANE SOCIETY OF THE UNITED STATES
WWF

June 30, 2017

U. S. Forest Service, Rocky Mountain Region
Attn: Regional Forester Brian Ferebee and Deputy Regional Forester Jacqueline Buchanan
1617 Cole Blvd.
Lakewood, CO 80401

RE: Follow-up to meeting on Thunder Basin National Grassland

Dear Mr. Ferebee and Ms. Buchanan,

We are writing in follow-up to our meeting with Ms. Buchanan on current and future collaborative efforts for sustainable management of Thunder Basin National Grassland's (TBNG) natural resources. We urge the Forest Service to move forward with implementation of the current TBNG Land and Resource Management Plan (2001), including the prairie dog management strategy as outlined in plan amendment #3 (2009). As long-term vested partners, we strongly believe that implementation of the current plan, which took extensive time, resources, input, and compromise from diverse stakeholders, is the clear way to move forward, as opposed to beginning another multi-year plan amendment process which we believe would not be in the best interest of any of the stakeholders as it would cause significant increased conflict.

We appreciate the opportunity to work with the Forest Service, the Ruckelshaus Institute working group, and livestock grazing permittees to find pragmatic solutions to prairie dog management. It is our hope that social conflicts can be reduced and all stakeholder interests addressed so together, we can move forward with our shared goal of maintaining grassland ecosystem health at Thunder Basin.

Thunder Basin National Grassland is one of the best remaining intact prairie ecosystems in the North American Great Plains. Prairie vestiges such as TBNG have become too few, small, degraded, and isolated from each other, which has contributed to significant losses in biological diversity. As conservationists, we are working to restore fully functioning, intact prairie ecosystems that sustain the array of wildlife associated with them. This ecosystem is home to many increasingly rare species of the prairie, including ferruginous hawk, swift fox, mountain plover, and burrowing owl. The reason these species flourish at Thunder Basin is due to the large complex of black-tailed prairie dog colonies found here, a once far more common occurrence across the Great Plains.

In addition, TBNG – lands within the public trust – are for multiple use, not just for those who live in proximity with ranching operations. Forest Service mandates account for managing for biodiversity as well as all stakeholder interests of these lands. The conservation of wildlife and the ecological health of this grassland is a shared value by all interests, prairie dogs aside.

Our request is simple: Implement the current TBNG Land and Resource Management Plan and prairie dog management strategy.

Our request includes:

- Maintaining Category 1 as key prairie dog habitat (with the minimum goal of 18,000 acres of active prairie dog colonies) and management area 3.63 for future recovery of the black-footed ferret;
- Utilizing nonlethal tools for prairie dog control measures where required or appropriate;
- Addressing other stakeholder concerns in compliance with plan standards and guidelines.

For nearly 12 years, our organizations have dedicated time, energy, and resources to prairie dog management at TBNG. Collectively, we have invested over $200,000 toward a host of conservation efforts on TBNG, including the relocation of prairie dogs away from private land boundaries into the core conservation area when acreage was below objective, as well as sylvatic plague mitigation and sylvatic plague research. To this end, we are advocating for solutions to address the current social climate related to management and control of prairie dogs. As Ms. Buchanan acknowledged during our meeting, the plan has not been properly executed given other Forest Service priorities in recent years. We are hopeful that implementation of the prairie dog and habitat management tools as outlined in the compromise plan, in addition to the collaborative vegetation management project currently being planned in one grazing allotment, will create more of a culture of collaboration and trust among the Forest Service and currently disparate stakeholders.

Our organizations are interested in continuing to work with the Forest Service to provide resources for the current plan’s implementation, including resources for willing landowners and grazing permittees to partner on habitat and wildlife restoration efforts on TBNG. Our key tasks provide for a successful approach toward these goals, as Forest Service partners.
These include:

- Working with the Forest Service and stakeholders to apply nonlethal prairie dog management practices;
- Identifying priority areas for habitat and wildlife restoration projects;
- Reaching out to landowners for cooperative agreements (along with securing resources) to implement habitat and wildlife restoration projects, such as with the Fiddleback Ranch, in cooperation with the Forest Service and Converse County;
- Assisting with black-footed ferret recovery when appropriate.

We believe these relationships and collaborations – working together for positive outcomes – are critical to moving forward for the health of TBNG.

We have heard directly that some stakeholders want a new plan amendment so that all mention of black-footed ferret recovery can be removed and fewer acres of prairie dogs maintained. However, these goals are clearly one-sided, unreasonable, and in violation of laws and policies requiring federal agencies to assist with listed species recovery. In addition, removing language or reference to black-footed ferrets and the potential for their reintroduction will not lead to more rainfall nor solve the current social issue with prairie dogs. Furthermore, the Forest Service does not have the funding to reduce prairie dogs down to the minimum acres required to be maintained under the current plan, let alone reduce even further. There is no need for a new plan amendment.

We firmly believe that moving forward with a new plan amendment process would be counter to achieving solutions and reducing conflict. The current plan and prairie dog amendment took 10 years to develop and included extensive public input and an appeals process. A directive for a new amendment would result in yet another costly and time intensive process for the Forest Service and for stakeholders and would inevitably lead to additional appeals and public controversy, stalling currently planned on-the-ground projects, adding more years to the already looming timeline, and delaying the important work to facilitate habitat improvements and prairie dog management on TBNG.

Instead of wasting valuable resources on an unnecessary and unworkable plan amendment, the Forest Service could work to reduce the social divide with prairie dog management. The full potential of the current plan has not been implemented.

Solutions must center on land uses and resource management activities that are conducted in a manner that is compatible with maintaining suitable black-footed ferret habitat. Standards listed in the TBNG Plan for (Chapter 3, Management Area 3.63, General – 1 (revised) include: 1) *Authorize only those uses and activities that do not reduce the suitability of the area as black-footed ferret reintroduction habitat; and 2) Manage all prairie dog colonies within this Management Area as though they were occupied by black-footed ferrets, and apply all Standards and Guidelines as though black-footed ferrets occupy all colonies*.

The 2009 plan amendment provides for the following:

- Category 1 Prairie Dog Habitat will have a "management objective of at least 18,000 acres of active prairie dog colonies."
- After exceeding 18,000 acres, any "use of rodenticide on federal lands may only be employed within ½ mile of the TBNG boundary and only in cases where appropriate and available nonlethal options have been tried and found ineffective for changing the rate and direction of colony expansion."
- Category 2 Prairie Dog Habitat have a combined (4W, Middleton, North 450, South Cellers and Piney Creek) management objective of 9,000 acres of active prairie dog colonies.

The current plan includes a suite of nonlethal measures (e.g., translocation, vegetative barriers, structural barriers, etc.) and lethal tools (rodenticide, shooting, etc.) to manage prairie dogs when they are below or above objective; in addition, the plan includes options for improving and restoring grassland habitat (e.g., cactus management, fire, etc.). Categories 1 and 2 represent a small portion of the overall acres of TBNG. The rest – upwards of 450,000 acres – is widely open to prairie dog lethal control. An estimated 100,000 prairie dogs are slated to be poisoned with the proposed 10,000 acres of poisoning in 2017 (10 prairie dogs per acre is widely accepted as a conservative estimate). This will also impact an unknown number of associated species. Under no circumstances should Rozol be approved for use within TBNG boundaries for the myriad of impacts it has on nontarget species.

We request the following actions:

- Immediately reinstate the shooting closure in Category 1 and Management Area 3.63;
- Ensure that Forest Service and county prairie dog control do not violate the TBNG plan;
- Prohibit the use Rozol on Forest Service lands; Rozol has proven impacts to nontargeted wildlife (please see appendix); the Western Association of Fish and Wildlife Agencies and the U.S. Fish and Wildlife Service also strongly oppose its use;
- Continue to encourage and help support habitat restoration projects with landowners;
- Provide for better inclusion of our organizations in discussions surrounding TBNG's prairie dog ecosystem.

We are currently soliciting the following for your information gathering efforts:

- Vegetation transects in the 3.63/Category 1 areas.
- 2) A prairie dog colony inventory and map (Thunder Basin Grassland Prairie Ecosystem Association).
- 3) The biological capability document for TBNG as a suitable black-footed ferret reintroduction site.

We include with this letter a map of prairie dog susceptibility to shooting beyond roads, eight articles related to the use of Rozol, showing impacts to non-target wildlife species, along with a summary of main points of those papers (complied by the Prairie Dog Coalition), and a memo on the current conditions relative to plague, with responses by Dr. David Augustine, USDA Agricultural Research Services.

We value the opportunity to provide comment for sustainable habitat and wildlife management practices on TBNG and toward our shared value of its ecological health. We would like to meet with you both as soon as possible to continue this important dialogue in person and provide additional ideas for solving conflicts while managing natural resources. Please let us know when you are available to meet.

Sincerely,

Chamois L. Andersen

Chamois L. Andersen
Senior Representative, Rockies and Plains Program, Defenders of Wildlife

Lindsey Sterling Krank
Environmental Scientist & Director, Prairie Dog Coalition, The Humane Society of the United States

Kristy LG Bly

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Shane Walker

UNITED STATES
ENVIRONMENTAL PROTECTION AGENCY
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OFFICE OF
PREVENTION, PESTICIDES AND
TOXIC SUBSTANCES

Potential Risks of Nine Rodenticides to Birds and Nontarget Mammals: a Comparative Approach

July 2004

Office of Pesticides Programs
Environmental Fate and Effects Division

Prepared by:

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Environmental Risk Branch 2

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Executive Summary

This document presents the Agency's assessment of potential risks to birds and nontarget mammals from 9 rodenticides, including 3 second-generation anticoagulants (brodifacoum, difethialone, bromadiolone), 3 first-generation anticoagulants (diphacinone, chlorophacinone, warfarin), and 3 non-anticoagulant compounds (zinc phosphide, bromethalin, cholecalciferol). These rodenticides are predominantly used to control commensal rats and mice in and around buildings, transport vehicles, and in sewers. Some, mainly zinc phosphide, chlorophacinone, and diphacinone, also have products registered for other outdoor uses against other rodent and small mammalian pests. A major concern in using rodenticides is that they are not selective to the target species; birds and nontarget mammals that feed on grain-based baits (pellets, meal, treated grains, wax blocks) or meat-based, vegetable, or fruit baits are potentially at risk. The available information from laboratory and pen studies, field studies, control programs, reported incidents, and toxicokinetics also indicates that a variety of avian and mammalian predators and scavengers are potentially at risk from consuming animals poisoned with some of these rodenticides.

The assessment focuses on the potential primary and secondary risks to birds and nontarget mammals posed by applications of these 9 rodenticides (11 baits) to control rats and mice in and around buildings (commensal use) and in field and other outdoor settings to control various rodent and other small mammalian pests. Risk is a function of exposure and hazard (toxicity), and data are available to estimate toxicity based on laboratory acute and secondary-hazard tests. However, typical use information used to estimate nontarget organism exposure, such as amount of active ingredient or formulated product applied per unit area, is not available for commensal uses. Thus, exposure estimates are largely based on the amount of active ingredient available per kilogram of the formulated bait (mg ai/kg bait). An assumption is made in most OPP/EFED risk assessments that birds and nontarget mammals are likely to be exposed to the pesticide via consumption of contaminated foods. This assumption is well established for rodenticides, for which ingestion of the formulated bait is the route of exposure.

Refining the exposure assessment to establish a quantitative measure of likelihood of exposure and effects would require a much more extensive data set than registrants have submitted for their rodenticides and for the nontarget species potentially at risk. The Agency provided the preliminary risk assessment to rodenticide registrants in October, 2001 and posted it in the EDocket on EPA's website for public comments from January 29 to May 30, 2003. No additional data or relevant information to refine the exposure assessment has been provided by the registrants or other stakeholders. Nevertheless, the existence of substantial incident data along with liver-residue analysis confirms that birds and nontarget mammals are being exposed and adversely affected by applications of rodenticide baits. The fact that numerous species of birds and mammals, including predators and scavengers, have been found exposed to these baits indicates that both primary and secondary exposures are occurring.

The risk conclusions are based both on the lines of evidence of the available data and comparative analysis modeling. Each rodenticide is ranked or categorized and compared to the other rodenticides according to the following criteria: (1) overall potential risk; (2) potential primary risk to birds; (3) potential primary risk to nontarget mammals; (4) potential secondary risk to avian predators and scavengers; and (5) potential secondary risk to mammalian predators and scavengers. Conclusions are presented below.

- Brodifacoum and difethialone stand out as the two rodenticides posing the greatest potential overall risk to birds and nontarget mammals, followed by bromadiolone and diphacinone. Zinc phosphide also ranked high for overall risk based on the comparative analysis modeling, primarily because of high potential primary risks.

- Brodifacoum, difethialone, and zinc phosphide pose the greatest potential primary risks to birds that eat bait. A single zinc phosphide or brodifacoum bait pellet provides more than an LD50 dose for a small bird. In contrast, a small bird would need to eat more than twice its body weight in bait pellets to ingest a comparable dose of a first-generation anticoagulant in a single feeding.

- Rodenticide baits are formulated to be lethal to small mammals, and they are not selective to the target species. All baits pose a high potential primary risk to nontarget mammals that eat bait. However, the first-generation anticoagulants likely pose less risk to mammals that only occasionally feed on 1 or just a few bait pellets, because they are more rapidly metabolized and generally must be eaten for several days to provide a lethal dose.

- Brodifacoum and difethialone pose the greatest potential risks to avian predators and scavengers that feed on target or nontarget animals poisoned with bait. The available data indicate that the first-generation anticoagulants are less hazardous than the more highly toxic and persistent second-generation anticoagulants.

- Mammalian predators and scavengers are at risk from feeding on animals poisoned with anticoagulant baits. Although the non-anticoagulant rodenticides appear to be much less hazardous to secondary consumers, confirmatory data are still needed to make this assumption for bromethalin and cholecalciferol baits.

- The available toxicokinetic data indicate that the second-generation anticoagulants are considerably more persistent in animal tissues than are the first-generation anticoagulants, and bioaccumulation may increase whole-body residues with repeat feedings.

- More than 300 documented wildlife incidents attest to exposure of birds and nontarget mammals, including endangered species, to some rodenticides, especially brodifacoum (244 incidents). Brodifacoum residue has been detected in liver tissue of 27 of 32 endangered kit foxes screened for rodenticide residues from 1999 to 2003. Birds in which rodenticides are most frequently detected include owls, hawks, eagles, and crows; mammals include wild canids and felids, tree squirrels, raccoons, deer, and others.

- The U. S. Fish and Wildlife Service issued a Biological Opinion in 1993 that includes reasonable and prudent alternatives and measures for protection of 29 mammalian and 11 avian threatened or endangered species potentially at risk from exposure to 8 of these rodenticides. These issues will be addressed by OPP's Endangered Species Protection Program.

- Adverse effects of possible sublethal exposure are unknown, and avian and mammalian reproduction studies are needed to establish a no-observable-adverse-effects concentration (i.e., "toxicity threshold") for each rodenticide.

A number of factors contribute uncertainty to the assessment. Those that appear to contribute the most uncertainty are: (1) missing data, including acute, chronic, and secondary toxicity as well as retention of some active ingredients in the liver, blood, and other body tissues; (2) the variable quality and quantity of existing data on metabolism and retention times in rodents and nontarget species; (3) specific use information by formulation, including typical amounts applied by use site, seasonally, and annually; distances applied from buildings; amounts used in rural versus urban areas; use by Certified Applicators versus homeowners and other non-certified applicators; and other such relevant information; (4) information on the number and species of birds and nontarget mammals frequenting baited areas and their likelihood of their finding and consuming bait or poisoned primary consumers in the various use areas; (5) methods to determine liver concentration(s) and total body burdens of rodenticide that would corroborate death or even if such a cause-effect relationship is appropriate (e.g., the "threshold of toxicity" concentration); (6) not accounting for the impacts of sublethal effects on reproduction and nontarget mortality (e.g., clotting abnormalities, hemorrhaging, stress factors including environmental stressors, such as adverse weather conditions, food shortages, and predation); (7) not accounting for bioaccumulation of repeated sublethal exposures to bait or poisoned rodents utilized as food by predators and scavengers; and (8) lack of incident reporting.

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Potential Risks of Nine Rodenticides to Birds and Nontarget Mammals: a Comparative Approach

Presented here is the Agency's assessment of rodenticide risks to birds and nontarget mammals. The 9 rodenticides include those addressed in the Reregistration Eligibility Decisions (REDs) for the Rodenticide Cluster (brodifacoum, bromadiolone, chlorophacinone, diphacinone, bromethalin; EPA 1998a), Zinc Phosphide (EPA 1998b), and Warfarin and its Sodium Salt (EPA 1991a). Difethialone and cholecalciferol, which are not subject to the current reregistration process but are alternative compounds for rat and mouse control, also are included. All 9 rodenticides are available to the public "over the counter" as grain-based food baits for control of commensal rats and mice, predominantly the Norway rat (*Rattus norvegicus*), roof rat (*R. rattus*), and house mouse (*Mus musculus*), in and around buildings, transport vehicles, and inside sewers. Some products, mostly "restricted-use" (i.e., available only to Certified Applicators) products containing zinc phosphide, chlorophacinone, or diphacinone, also are available for control of various rodent and other small mammal pests in field and other outdoor settings.

The purpose of this assessment is to evaluate potential primary and secondary risks of each rodenticide and to compare and rank them among compounds. The Agency's concern about risks to birds and nontarget mammals is based on several factors, including (1) the high acute toxicity of these rodenticide baits, which are designed to be lethal to small mammals; (2) risk estimates, based on available exposure and toxicity data, that exceed Agency levels of concern (LOCs); (3) mortality of birds and nontarget mammals exposed to rodenticide baits or poisoned prey in laboratory, pen, and field settings; (4) retention time of residues in body tissues of primary consumers, and (5) numerous reported incidents that indicate exposure of numerous nontarget species, including avian and mammalian predators and scavengers. Rodenticide baits are formulated to be lethal to rodents and a few other small mammals, and they are not selective to target species. Many factors influence which nontarget animals might be exposed to baits, but many birds and mammals are attracted to seeds and grains and are likely to consume grain-based baits. A few commensal baits also contain flavorizers such as fish, molasses/peanut butter, or apple, and some field baits are formulated with foods other than grains (ground meat, canned or dry meat-based pet foods, fruits, vegetables) that might appeal to carnivores and omnivores. Rodenticide baits also pose potential secondary risks, because predators and scavengers are likely to be attracted to dead or dying rats, mice, and poisoned nontarget animals.

Risk is a function of exposure and hazard (toxicity). Data are available to estimate toxicity based on laboratory acute-toxicity and secondary-hazard tests. Use information, such as amount of active ingredient or formulated product applied per unit area per application, is typically used to estimate nontarget organism exposure but is not available for most rodenticide uses. Therefore, exposure estimates are largely based on the amount of active ingredient available per kilogram of grain-bait formulation (mg ai/kg bait, or ppm ai). See the "*Exposure*" section under

"*Use and Exposure Considerations*" for additional discussion of the differences in estimating expected environmental concentrations (EECs) for rodenticide food baits versus other types of pesticide applications (e.g., foliar sprays).

Risk conclusions are presented in tabular and graphical form based on two analyses of the available data. One analysis is a ranking of potential risks of each rodenticide based on a comparative analysis model. That methodology is explained in more detail in the "*Comparative analysis model*" section of the assessment and in Appendix C. The other analysis uses a lines-of-evidence approach in which the available quantitative and qualitative information is evaluated and each rodenticide assigned a rating of high, moderate, or low for primary risk to birds, primary risk to mammals, secondary risk to birds (avian predators and scavengers), and secondary risk to mammals (mammalian predators and scavengers). For primary risks, the amount of bait and number of bait pellets that need to be eaten to provide an LD50 dose (i.e., dose expected to be lethal to 50% of the individuals in a population) are calculated for 3 size classes (25 g, 100 g, 1000 g) of birds and mammals. Dietary risk quotients that compare the amount of toxicant (ppm ai) in a bait to the dietary toxicity (LC50) of the rodenticide also are used as a comparative index of primary risk. For secondary risks, these methods cannot be used, because LD50 and LC50 data are not available for predatory species of birds and mammals. Consequently, assessments of secondary risk are made based on mortality and other adverse effects reported in laboratory and field studies and operational control programs, incident reports, toxicokinetic data, and residues reported in primary consumers. This approach is in accord with EPA's risk-assessment guidelines (EPA 1998c), which assert that professional judgement or other qualitative evaluation techniques are appropriate for ranking risks into categories such as low, medium, and high when exposure and effects data are limited or are not easily expressed in quantitative terms. A lines-of-evidence approach for improving field-study interpretation also has been advocated by the Avian Effects Dialogue Group (Rymph 1994).

The information used in this assessment was obtained from studies submitted to the Agency in support of registration/reregistration, from published literature and personal communications, and from the Agency's Ecological Incident Information System (EIIS). For some rodenticides, few data are available other than acute oral (LD50) and dietary toxicity (LC50) values for the Agency's required test species: northern bobwhite (*Colinus virginianus*), mallard (*Anas platyrhynchos*), and laboratory rat (*R. norvegicus*). The quality and quantity of data available on metabolism and retention times in rodents and secondary toxicity to nontarget birds and mammals vary among the rodenticides, but the available data are sufficient to identify the most persistent and hazardous compounds.

Modes of action

The anticoagulant rodenticides are vitamin-K antagonists that disrupt normal blood-clotting mechanisms and induce capillary damage (Pelfrene 1991). Death results from hemorrhage, and exposed animals may exhibit increasing weakness prior to death. Behavior also may be affected (Cox and Smith 1992). The anticoagulants are typically grouped into "first-generation" (warfarin, chlorophacinone, diphacinone) and "second-generation" (brodifacoum, bromadiolone, difethialone) compounds. Second-generation anticoagulants tend to be more acutely toxic than are the first-generation anticoagulants, and they are retained much longer in body tissues of primary consumers. They generally provide a lethal dose after a single feeding, although death is usually delayed 5 to 10 days and animals continue feeding. In contrast, the first-generation compounds, because they are less acutely toxic and more rapidly metabolized and/or excreted, generally must be ingested for several days to provide a dose lethal to most individuals. Diphacinone and chlorophacinone may kill some animals in a single feeding, but multiple feedings are generally needed for sufficient population control (Timm 1994). The structural relationships of these rodenticides and some of their physical/chemical properties are presented in Attachment A.

The non-anticoagulant rodenticides belong to 3 chemical classes that differ from one another and the anticoagulants in their mode of action. They can provide a lethal dose from a single feeding but are much less likely than the anticoagulants to be retained in toxicologically significant amounts in body tissues of primary consumers. Bromethalin, a diphenylamine, is a neurotoxicant that causes respiratory arrest from inadequate nerve impulse transmission after fluid build-up and demyelination inside the central nervous system (Spaulding and Spannring 1988, Hyngstrom et al. 1994). Further feeding is inhibited after ingestion of a lethal dose, and death typically occurs within 2 days. Zinc phosphide is an inorganic compound whose toxicity results from liberation of phosphine gas from reaction of the active ingredient with water and acid in the stomach (Hyngstrom et al. 1994). Death can occur within a few hours of ingestion. Cholecalciferol is a sterol (vitamin D_3). Its ingestion results in hypercalcemia from mobilization of calcium from bone matrix into blood plasma (Pelfrene 1991). Death can occur 3 to 4 days after a single feeding.

Terms and definitions

Dietary toxicity test: To support registration of a pesticide, the Agency's Office of Pesticides Program (OPP), Environmental Fate and Effects Division (EFED), requires 2 avian dietary (LC50) studies: one using northern bobwhite chicks as test animals and the other using mallard ducklings (40 CFR §158.490 Wildlife and Aquatic Organisms Data Requirements, Guideline Reference No. 71-2). The dietary test consists of a 5-day exposure period during which toxicant is added to the birds' diet at 5 concentrations using 10 test animals (5 males, 5 females) per concentration. The exposure period is followed by a 3-day observation period; however, because death is delayed for several days after exposure to an anticoagulant, the post-treatment observation period has been extended 15 days or more for those compounds. The test material is the technical grade of the active ingredient.

Dietary toxicity testing is not usually conducted for mammals, although the Agency may require a wild-mammal toxicity test (40 CFR §158.490 Wildlife and Aquatic Organisms Data Requirements, Guideline Reference No. 71-3) if deemed necessary. Because rodenticides are formulated to be lethal to mammals and the Agency requires efficacy testing for all rodenticide end-use products (40 CFR §158.640 Product Performance Data Requirements, Guideline Reference No. 96-10 and 96-12), EFED has not required a wild-mammal toxicity test for any of the rodenticides. However, EFED has found reports for laboratory-rat dietary tests for 5 rodenticides tested by the Agency's former Toxicology Unit, Chemical and Biological Investigations Branch. During 1980 and 1981, McCann et al (1981) developed a short-term dietary LC50 test for small mammals. They exposed 5-male and 5-female immature albino Norway rats (Wistar strain) per test concentration to dry diet offered *ad libitum* and treated with one of 17 chemicals pesticides, mostly organophosphate and carbamate pesticides. The tests consisted of a 5-day acclimation period, a 5-day exposure period, and a post-treatment observation period lasting at least 9 days. Following submission of the paper for publication, testing continued and included 5 rodenticides: brodifacoum, bromadialone, chlorphacinone, diphacinone, and warfarin. Results of these tests were not published but the test reports are available, and multiple studies exist for each of those 5 rodenticides.

LC50: Median lethal concentration. A statistically estimated dietary concentration expected to be lethal to 50% of the test animals. The LC50 is expressed in ppm. The 95% confidence intervals are reported when available.

Acute oral toxicity test: For individual pesticides, EFED requires one acute oral (LD50) test for birds, using either the northern bobwhite or the mallard as the test species (40 CFR §158.490 Wildlife and Aquatic Organisms Data Requirements, Guideline Reference No. 71-1). Data are available for both species for some rodenticides. The toxicant is orally administered via capsule or gavage in a single dose to adult animals. The test required by the Agency includes 5 concentrations, with 10 test animals (5 males, 5 females) per concentration. Unless otherwise noted, the test material is the technical grade of the active ingredient. OPP's Health Effects Division (HED) also requires acute oral testing with the laboratory rat (40 CFR §158.340 Toxicology Data Requirements, Guideline Reference No. 81-1) and sometimes has data for other mammals (e.g., laboratory mouse, dog). EFED uses these data in the mammalian risk assessment.

LD50: Median lethal dose. A statistically estimated oral dose expected to be lethal to 50% of the test animals. The LD50 is expressed in mg of active ingredient per kg of body weight of animal. The 95% confidence intervals are reported when available.

> ***Note:*** Some LD50 values for birds and mammals were obtained from the literature. These are considered supplemental data, because the test concentrations, number of animals tested, and confidence intervals often are not reported or may not meet Agency test guideline requirements. Calculations of risk quotients and estimates of ingestion of active ingredient from bait consumption utilize the toxicity data reviewed and accepted by the Agency.

Primary Risk: Risk to target or nontarget organisms that consume bait.

Secondary Risk: Risk to predatory or scavenging birds or mammals that feed on target or nontarget animals that ate bait.

Dietary Risk Quotient (RQ): An index of exposure to dietary toxicity (LC50), where exposure is expressed as the amount of rodenticide in food (ppm ai in bait for primary exposure or in target species for secondary exposure). Risk presumptions are based on whether or not RQs exceed OPP's Levels of Concern. RQs do not quantify risk, but they are useful for comparing risks among alternative compounds (ECOFRAM 1999).

Level of Concern (LOC): A presumption of risk is made if an RQ equals or exceeds the Agency's LOCs: 0.5 for acute risk to non-endangered species and 0.1 for acute risk to endangered species. Additionally, an RQ that equals or exceeds 0.2 triggers consideration of "restricted-use" classification to mitigate acute risk.

***A note on scientific names*:** The scientific name of a species is provided after the first mention of its common name in the text. A complete list of common and scientific names of the birds and mammals referred to in the document is included in Attachment B.

Comparative analysis model

A comparative analysis model also is used to rank and compare potential primary and secondary risks. The underlying methodology is a simple multi-attribute rating technique, or SMART (Goodwin and Wright 1998). SMART is adapted for comparing potential risks among rodenticides based on a number of measure-of-effect values for primary and secondary risk to birds and mammals. Each type of risk is quantitatively evaluated by the following measures of effect:

Primary risk to birds:	dietary RQ (mean value if more than one dietary RQ available); inverse of the number of bait pellets needed for a 100-g bird to ingest an LD50 dose in a single feeding
Primary risk to mammals:	inverse of the number of bait pellets needed for a 100-g mammal to ingest an LD50 dose in a single feeding
Secondary risk to birds:	mean % mortality from secondary toxicity studies; retention time (days) of active ingredient in the blood; retention time (days) of active ingredient in the liver
Secondary risk to mammals:	mean % mortality from secondary toxicity studies; retention time (days) of active ingredient in the blood; retention time (days) of active ingredient in the liver

Retention time is not a direct measure of effect for secondary risk to birds and mammals, but it is an important contributing factor. The combination of mean % mortality from secondary laboratory toxicity studies, which characterizes the secondary toxicity from short-term exposures, and available data on retention time in both blood and liver, which indicates how long toxic levels can persist in target animal tissues, can characterize the secondary risk to birds and mammals.

When faced with a number of alternatives and a number of types of risk with measures of effect, SMART prescribes the following: (1) each alternative rodenticide is rated on each measure of effect; (2) each measure of effect is assigned a measure of importance to the risk assessor; and (3) a summary score for each alternative rodenticide is calculated as a weighted average of the ratings, where the weights represent the relative importance of the measure of effect for each type of risk. The higher the resultant summary score, the higher the potential risk for that rodenticide.

The following basic equation is used to calculate the summary values for the risk comparison:

$$\text{Summary Value}_{(\text{scale from 0 to 10})} = 3\ ƒ(\mathrm{ME}_i)(\mathrm{ME}_{max})^{-1}„\ ƒ(\text{Weight})\ (3\text{Weights})^{-1}„\ (10)$$

where "ME_i" is the measure of effect value for a rodenticide and "ME_{max}" is the maximum ME for all rodenticides; "Weight" is the importance value, from 10 to 0, placed on each measure of effect, with high = 10 to 6.67, medium = 6.68 to 3.33, and low = 3.34 to 0; "3Weights" is the sum of all the weights for all the measures of effect. All measures of effect, except two, are assigned a "high" (10 out of 10) measure of importance for the rodenticide analysis. The half-life in blood and liver are each given a weight of "low" (2.5 out of 10) for analyzing secondary risks to birds and mammals, so that the overall importance of the persistence data (2.5 x 4=10) equals but does not exceed that of the mortality data.

A sensitivity analysis also is performed to evaluate how changes in each measure-of-effect value could affect the overall summary risk results. Each measure-of-effect value is separately decreased and increased by 50% (154 variations). To further examine the robustness of the rankings, selected high and low summary risk values are subsequently changed by up to ±99%. Further details of the SMART analysis, including the input values for measures of effects, are presented in Attachment C.

The methodology used in the comparative analysis model is similar to that used in the Agency's "Comparative Analysis of Acute Risk From Granular Pesticides" (EPA 1992) and "A Comparative Analysis of Ecological Risks from Pesticides and Their Use: Background, Methodology, Case Study" (EPA 1998d); both were reviewed by a FIFRA Scientific Review Panel. Concerning the latter analysis, the Panel noted the many scientific uncertainties in the method, yet agreed that it was a useful screening tool that provides an estimate of relative risk. The Panel made a number of helpful suggestions to improve the utility of the method, most of which are included here. In this analysis, a risk quotient (RQ), calculated as the ratio of toxicant potentially ingested to the inherent toxicity of the rodenticide, is used to compare potential primary risks to birds and nontarget mammals. RQs are compared among rodenticide baits based on the amount of bait and number of bait pellets that birds or nontarget mammals of various sizes would need to eat to ingest an acute oral (LD50) dose. Dietary data (LC50) also are available, and RQs based on bait concentration and avian dietary toxicity are compared among the rodenticides. As noted by the Ecological Committee on FIFRA Risk Assessment Methods (ECOFRAM 1999), RQs do not quantify risk but are useful for comparisons among alternative compounds. EPA's "Guidelines for Ecological Risk Assessment" (EPA/630/R-95/002F, 1998c) also notes that quotients provide an efficient, inexpensive means of identifying high- or low-risk situations that can allow risk management decisions to be made without the need for further information.

Use and Exposure Considerations

This assessment focuses on the potential primary and secondary risks to birds and nontarget mammals posed by applications of these 9 rodenticides to control rats and mice in and around buildings (commensal uses) and elsewhere outdoors (field uses) to control rodents and certain other mammalian pests. As previously noted, rodenticide products for field use (except those for underground baiting of pocket gophers and moles) are currently registered as "restricted-use" or restricted-use classification is being imposed during reregistration. This classification provides increased protection of birds and nontarget mammals, because baits may only be applied by a Certified Applicator or someone directly supervised by a Certified Applicator. These applicators are trained to closely follow label use directions and restrictions that may help limit exposure, and thus risk, to nontarget organisms. However, even with this increased protection, there remains a potential risk to nontarget organisms from these uses since the rodenticides are lethal to birds and mammals, are not selective, and their grain-based bait formulations may be highly attractive to many nontarget organisms.

Product labels for commensal uses specify that applicators should comply with the following *DIRECTIONS FOR USE*:

> "Apply bait in locations out of reach of children, pets, domestic animals and nontarget wildlife, or in tamper-resistant bait stations. These stations must be resistant to destruction by dogs and by children under 6 years of age, and must be used in a manner that prevents such children from reaching into bait compartments and obtaining bait. If bait can be shaken from stations when they are lifted, units must be secured or otherwise immobilized. Even stronger bait stations are needed in areas open to hoofed livestock, raccoons, bears, or other potentially destructive animals, or in areas prone to vandalism."

To what extent applicators comply with these use directions or even use bait stations is unclear. As noted in Pesticide Regulation (PR) Notice 94-7 (EPA 1994), "Nonprofessional users (i.e., the "general public") often apply baits in open containers or in ready-to-use, non-protective, packaging. Bait stations typically are not offered for sale at the outlets where nonprofessional users buy rodenticides. Attempts to market ready-to-use (bait-filled) protective rodenticide bait stations to the general public have not been reported as commercially successful ventures." Tamper-resistant or stronger bait stations exclude mammals larger than adults of the target species, because the entrance holes to the bait compartment are designed to be no larger than necessary. However, mammals smaller than the target species can enter bait stations and feed on bait and are at risk. Because target species leave bait stations after feeding, bait stations likely have little if any impact on secondary exposure of predators and scavengers that feed on dead or dying rodents.

The commensal use in and around buildings is common to all 9 rodenticides. However, difethialone and bromadiolone can be applied only inside of buildings and similar manmade structures in non-urban areas. Indoor applications likely reduce primary exposure of nontarget organisms. Nevertheless, rats or mice that eat bait, especially an anticoagulant bait, do not die for several days after ingesting a lethal dose. Because these target species may move outdoors before dying, some predators and scavengers might still be exposed as a result of indoor application.

Field uses involve a variety of bait applications, including broadcasting, spot-baiting, or application of bait in some type of bait station. Depending on the use, broadcasting is done by hand, ground-based mechanical spreader, or by air. Some, but not all, broadcast applications limit the number of treatments that can be made and specify an interval between applications. Some uses also allow spot baiting, in which bait is placed by hand in small pile or scattered across smaller areas (e.g., bare ground around burrow openings) at a treatment site. Bait stations should be covered or enclosed. For some uses an uninterrupted supply of bait is maintained for 1 to 4 weeks, whereas for others no time interval is specified. Bait stations are usually placed on the ground in areas frequented by the target species, such as by burrow openings, runways, or feeding areas. Floating bait stations are used for some target species (e.g., muskrats). In some situations, customized bait stations have been developed to exclude nontarget species that are smaller than individuals of the target species. Elevated and "T" bait stations have been developed to reduce exposure of some nontarget species, such as deer mice (Erickson et al. 1990) and kangaroo rats (California Department of Pesticide Regulations
http://www.cdpr.ca.gov/docs/es/espdfs/baitsta1.pdf
http://www.cdpr.ca.gov/docs/es/espdfs/baitsta2.pdf).
More research is warranted to devise means of selectively applying baits to protect nontarget species while adequately maintaining efficacy against target species.

For control of pocket gophers and moles in lawns, golf courses, and other noncrop areas, bait is applied in subsurface runways or deeper underground tunnels and is not exposed on the ground surface. Hand baiting is done using a mechanical probe or similar device to locate an underground runway. Bait is inserted through the probe hole, and the hole is then sealed with sod or a stone. In some situations a mechanical burrow-builder is used by a Certified Applicator to construct artificial pocket-gopher burrows into which bait is mechanically inserted at 4- to 5-foot intervals.

Exposure

Exposure is an integral component of ecological risk. Many factors influence which nontarget animals might be exposed to rodenticide baits. They include the species found in and around treatment areas, species' food habits and foraging behavior, home range, propensity to feed in and near human buildings, bait availability (e.g., quantity, how applied, where applied, when applied), and other such factors. However, there is no doubt that many birds and nontarget mammals are attracted to and will consume grain-based foods. Additionally, many nontarget predators and scavengers feed on rats, mice or other target species. They are not likely to avoid feeding on rats, mice, voles, ground squirrels, or other animals that have eaten bait.

EFED's exposure assessment for the rodenticides differs from that for most other pesticides. For foliar-applied pesticides, EECs on potential food items (grasses, seeds, insects) of birds and mammals are extrapolated from field-residue data compiled by Hoerger and Kenaga (1972) as modified by Fletcher et al. (1994). The maximum EEC on avian and mammalian food items is 240 ppm on short grass, 135 ppm on broadleaf plants and insects, and 15 ppm on seeds for every 1.0 lb ai applied per acre. EECs for granular formulations or soil-applied sprays are typically based on the number of LD50s applied per square foot. For each specific crop or use site, EECs depend on the label-specified application rate (lb ai/acre), number of applications, interval between applications, and the application method. However, for a rodenticide, the bait itself is the potential food item of concern. Thus, the amount of active ingredient in the formulated bait is used as the EEC. This information is used to estimate the amount of bait and number of bait pellets that birds and mammals of various sizes need to consume in a single feeding to obtain a dose expected to be lethal to 50% of the individuals in the population (i.e., LD50 dose). Estimates of food-ingestion rates (g dry matter per day) were determined from established allometric equations presented in EPA's Wildlife Exposure Factors Handbook (EPA 1993). The concentrations of active ingredient in the bait pellets are also used to estimate initial dietary exposure (mg ai per kg in bait) used to calculate avian and mammalian dietary risk quotients.

These estimates of acute primary exposure of nontarget organisms are not appropriate for estimates of secondary exposure. Secondary exposure estimates are considerably more complex and require consideration of residues in tissues of target organisms that are commonly consumed by predators and scavengers, as well as knowledge of what residue level will result in mortality or adverse chronic effects. Moreover, it is important to know how long the residue persists in body tissues. A number of laboratory tests using avian and mammalian predators or scavengers are available to assess mortality from secondary exposure resulting from consumption of prey animals that had been exposed to rodenticides. Design and methodology vary among studies, adding unknown variability to the results and analysis. Pending development of standard methods and testing requirements for such studies, these tests provide the best data available. The mean percent (%) mortality for these bird and mammal laboratory tests are used to estimate both secondary exposure and hazard. Because retention time in tissues consumed by scavengers and predators is an important factor in estimating secondary exposure and potential risk, available retention times (half-life in days) of rodenticide in liver and blood are also factored into secondary exposure and risk estimates. A discussion of residue levels in tissues of target species is included in the assessment. Uncertainties remain in establishing levels indicative of mortality or other adverse effects in nontarget organisms.

In most pesticide assessments the assumption is made that nontarget birds and mammals are likely to be exposed to the pesticide without attempting to establish a quantitative measure of this likelihood. This assumption is used in this assessment for these 9 rodenticides and 11 bait formulations. The existence of substantial incident data along with liver residues corroborates the assumption that nontarget birds and mammals are exposed and adversely affected by the use these rodenticide baits. The fact that numerous species have been found exposed to these rodenticide formulations, including predators and scavengers, indicates that both primary and secondary exposure occurs.

Target species, use sites, and rodenticide usage

Control of commensal rats and mice is the predominant use of most of the rodenticides. Most products for rat and mouse control are formulated as grain-based pellets or, for sewer use, as paraffinized food blocks. Several rodenticides also are registered for field and other outdoor uses (Table 1). Zinc phosphide is used to control ground squirrels (*Spermophilus* spp.), prairie dogs (*Cynomys* spp.), pocket gophers (Geomyidae), and moles (Talpidae) in addition to commensal rats and mice. Most are pellets or grain baits, but meat (ground meat, canned dog or cat food, dry meat-based pet food), sunflower seed, and fruit or vegetable (carrots, sweet potatoes, dandelions, alfalfa, beet tops, cabbage, potatoes, grapes, mulberry, apricots, figs, nuts, apples, pears) baits also are used against some target species. Nine states also have individual state registrations (FIFRA §24c Special Local Need [SLN]) for using zinc phosphide to control a variety of localized rodent (e.g., voles, tree squirrels, kangaroo and other rats, deer mice, muskrats, nutria) and jackrabbit pests. Brodifacoum and bromethalin are or have been used under emergency exemptions (FIFRA §18) to control introduced rats on U. S. islands in the Pacific Ocean. Twenty-three states have SLNs for chlorophacinone and/or diphacinone, mostly to control meadow voles (*M. pennsylvanicus*) and/or pine voles (*M. pinetorum*) in orchards or ground squirrels in rangeland or other uncultivated areas. Other limited uses include control of mongooses (*Herpestes auropunctatus*) in Hawaii, voles in small-grain crops in Washington, and a variety of other rodent pests and jack rabbits (*Lepus* spp.) in California. New Mexico uses cholecalciferol to control rock squirrels (*Spermophilus variegatus*).

Table 1. Commensal and Field Uses of Rodenticides in the United States (adapted from EPA 1998a,b)

Rodenticide	Date ai registered	Commensal uses	Field and other outdoor uses	mg ai/kg bait (ppm)
Second-generation anticoagulants				
Brodifacoum	1979	Rat and mouse control in and around buildings, transport vehicles, and inside sewers	Restricted-use applications for rat control on some oceanic islands (FIFRA §24c Special Local Needs [SLN] or FIFRA §18 emergency exemption)	50 25 (Anacapa Island, CA)
Difethialone	1995	Rat and mouse control in and around buildings in urban areas; limited to indoor use in non-urban areas	None	25
Bromadiolone	1980	Rat and mouse control in and around buildings, transport vehicles, and inside sewers in urban areas; limited to indoor use in non-urban areas	None	50
First-generation anticoagulants				
Chlorophacinone	1971	Rat and mouse control in and around buildings and inside sewers	Control of pocket gophers and moles in underground burrows; SLNs for control of pine and/or meadow voles in orchards (17 states), ground squirrels in rangeland and around burrows (8 states), jack rabbits (CA, OR), and a variety of other field rodents (e.g., deer mice, woodrats, muskrats) in CA	50 100 (some field uses) other[a]

Rodenticide	Date ai registered	Commensal uses	Field and other outdoor uses	mg ai/kg bait (ppm)
Diphacinone	1960	Rat and mouse control in and around buildings and inside sewers	Control of pocket gophers in underground burrows; SLNs for control of pine and/or meadow voles in orchards (16 states), ground squirrels in rangeland and around burrows (6 states), a variety of other field rodents (e.g., deer mice, woodrats, muskrats) and jack rabbits in CA, various field rodents in several other states, rat control on oceanic islands (HI, AK), and mongoose control (HI)	50 100 (some field uses) other[a,b]
Warfarin	1950	Rat and mouse control in and around buildings	Deer mouse and white-footed mouse control in and around buildings and in bait stations in other areas such as parks and woodlots	250 other[b]
Others (non-anticoagulants)				
Bromethalin	1984	Rat and mouse control in and around buildings, transport vehicles, and inside sewers	Restricted-use application for rat control on an oceanic island (emergency exemption)	100
Zinc phosphide	1940s	Rat and mouse control in and around buildings[a]	For control of a wide variety of field rodents (e.g., ground squirrels, prairie dogs, voles, rats, kangaroo rats, deer mice, moles, pocket gophers) in various sties, including rangeland, uncultivated areas, orchards, turf, forage, sugarcane, and other sites; 9 states also have SLNs for use against various rodents at local use sites	20,000 10,000 (CA only)
Cholecalciferol	1984	Rat and mouse control in and around buildings and inside transport vehicles	SLNs for control of rock squirrels (NM); also roof rats on an oceanic island (CA)	750

[a] chlorophacinone (0.2% ai), diphacinone (0.2% ai), and zinc phosphide (10% ai) tracking powders are registered for indoor use and inside burrows along building foundations; all are restricted-use products

[b] sodium salts of diphacinone and warfarin are registered for use in water baits for indoor use only

Adequate information quantifying usage of rodenticide baits is lacking. EPA obtains data on the amount of each product produced annually, and the Rodenticide Registrants Task Force (RRTF) provided some limited information on the pounds of active ingredient produced or imported in 1996 and 1997 for 4 of the 9 rodenticides (Kaukeinen et al. 2000). However, these data provide no information on when, where, or how the products are used and thus provide little relevant information for assessing exposure and risk. The RRTF data are difficult to interpret, because they lump containers and placement units, even though containers differ, often considerably, from placement units. A placement for commensal rodents is defined on product labels as 3 to 16 oz of bait for rats and 0.25 to 0.5 oz of bait for mice. In contrast, containers can hold anywhere from several to many individual rat or mouse placements. The problem with lumping these units together is illustrated in Table 2. Both brodifacoum and bromadiolone, for example, are formulated as 0.005% ai food baits solely for commensal rat and mouse control. The data for 1996 indicate that 395 lb ai of brodifacoum was formulated into more than 40 million "container/placement units" (i.e., 3 oz bait per container/placement unit), whereas 233 lb ai of bromadiolone was formulated into few more than 275,000 container/placement units (i.e., 271 oz bait per container/placement unit). Such differences also occur for 1997 and for chlorophacinone and diphacinone. Refining the exposure assessment would necessitate much better information for each rodenticide, including the amount of bait applied annually and seasonally; geographically by state or region; in field settings versus in and around buildings; in urban versus suburban and rural locales; indoor versus outdoor placements; applications for rats versus those for mice; use by the general public versus that by Certified Applicators; proportion of bait placements made in tamper-resistant bait stations; and, for chlorophacinone and diphacinone, use of 0.005% versus 0.01% ai baits.

Table 2. Amount of Bait and Number of "Container/Placement Units" For Four Anticoagulant Rodenticides in 1996 and 1997 (adapted from Kaukeinen et al. 2000). Information was not provided for difethialone, warfarin, or the non-anticoagulants.

Anticoagulant[a]	Year	lb ai[b]	oz bait[c]	no. containers/ placement units[b]	oz bait per container/ placement unit
Brodifacoum	1996	395	126,400,000	40,895,724	3
	1997	441	141,120,000	44,144,456	3
Bromadiolone	1996	233	74,560,000	275,376	271
	1997	164	52,480,000	294,706	178
Diphacinone	1996	486	155,520,000	1,551,161	100
	1997	608	194,560,000	2,860,419	68
Chlorophacinone	1996	1608	514,560,000	21,552	23,875
	1997	2677	856,640,000	18,360	46,658

[a] brodifacoum and bromadiolone are registered only for control of commensal rats and mice; diphacinone and chlorophacinone are registered for commensal rats and mice and are also used for control of field rodents in rangelands, orchards, and other settings

[b] data from Kaukeinen et al. 2000

[c] based on 0.005% ai food baits

Primary-hazards Data

Birds

Acute-oral and dietary toxicity: The available acute-oral and dietary toxicity data for birds are presented in Tables 3, 4, and 5. LC50 values for the northern bobwhite and mallard, required test species for EPA/OPP avian guideline studies, are used in calculating dietary RQs. The bobwhite or mallard LD50 also is used to calculate the amount of bait and number of rat-bait pellets that birds of various sizes need to eat to ingest a dose lethal to 50% of the individuals in the population. Some toxicity data also are available for other species for some rodenticides. Most of those values (e.g., Godfrey 1986) were determined using fewer test concentrations and fewer test animals per concentration than are required for EPA guideline studies. EFED considers these values as supplemental data that provide additional characterization of avian toxicity.

Table 3. Acute Oral and Dietary Toxicity of Second-generation Anticoagulants to Birds

Rodenticide/ Species	LD50, mg/kg (95% CI)	LC50, ppm (95% CI)	Reference
Brodifacoum			
Northern bobwhite		0.8 (0.1-4.7)	EPA 1998a
Mallard	0.26 (0-0.8)	2.0 (0.8-4.8)	EPA 1998a
Laughing gull		0.7	ICI 1979a
Laughing gull		1.6 (0.8-3.3)	ICI 1979b
Canada goose	<0.75[a]		Godfrey 1986
Black-backed gull	<0.75[a]		Godfrey 1986
Purple gallinule	0.95		Godfrey 1986
California quail	3.3		Godfrey 1986
Mallard	4.6		Godfrey 1986
Black-billed gull	<5[a]		Godfrey 1986
Ring-necked pheasant	10		Godfrey 1986
Australasian harrier	10		Godfrey 1986
Blackbird	>3[b]		Godfrey 1986
Hedge sparrow	>3[b]		Godfrey 1986
House sparrow	>6[b]		Godfrey 1986
Difethialone			
Northern bobwhite	0.26 (0.17-0.40)	0.56 (0.16-1.91)	EFED[c]
Mallard		1.4 (0.7-5.1)	EFED[c]
Bromadiolone			
Mallard		158 (7-762)	EPA 1998a
Mallard		440 (229-847)	EPA 1998a
Northern bobwhite	138 (81-235)	37.6 (9-85)	EPA 1998a
Northern bobwhite	170 (115-261)		EPA 1998a

[a] the lowest concentration tested

[b] the highest concentration tested

[c] OPP/EFED Toxicity Database

Table 4. Acute Oral and Dietary Toxicity of First-generation Anticoagulants to Birds

Rodenticide/ Species	LD50, mg ai/kg (95% CI)	LC50, ppm (95% CI)	Reference
Chlorophacinone			
Mallard		172 (75-498)	EPA 1998a
Northern bobwhite	258 (167-356)	56 (22-105)	EPA 1998a
Ring-necked pheasant	>100		Clark 1994
Red-winged blackbird	430		Clark 1994
Diphacinone			
Mallard	3158 (1605-6211)	906 (187-35,107)	EPA 1998a
Northern bobwhite	400 < LD50 <2000	>5000	EPA 1998a
Warfarin			
Mallard	620	890 (480-1649)	EFED[a]
Northern bobwhite	>2150	625 (300-1303)	EFED[a]
Chicken (domestic)	942		Bai and Krishnakumari 1986

[a] OPP/EFED Toxicity Database

Table 5. Acute Oral and Dietary Toxicity of non-Anticoagulant Rodenticides to Birds

Rodenticide/ Species	LD50, mg ai/kg (95% CI)	LC50, ppm (95% CI)	Reference
Bromethalin			
Northern bobwhite	4.6 (3.6-5.8)	210 (150-280)	EPA 1998a
Northern bobwhite	11.0 (9.3-13.1)		EPA 1998a
Mallard		620 (460-820)	EPA 1998a
Chicken (domestic)	8.3		HED[a]
Zinc phosphide			
Northern bobwhite	12.9 (12.0-13.9)	469 (356-546)	EPA 1998b
Mallard	35.7 (11.8-108)	1285 (1026-1620)	EFED[b]
Mallard	67.4 (56.3-80.9)	2885 (1970-4329)	EPA 1998b
Mallard	13		CDFG 1962[c]
White-fronted goose	7.5		CDFG 1962[c]
Snow goose	8.8		CDFG 1962[c]
Ring-necked pheasant	8.8		CDFG 1962[c]
Canada goose	12.0		CDFG 1962[c]
California quail	13.5		CDFG 1962[c]
Gray partridge	26.7		Janda and Bosseova 1970
Ring-necked pheasant	26.7		Janda and Bosseova 1970
Red-winged blackbird	23.7		Clark 1994
Mourning dove	34.3		CDFG 1962[c]
Horned lark	47.2		EFED[b]
Golden eagle	>20		EFED[b]
Cholecalciferol			
Northern bobwhite		528[d]	EFED[b]
Mallard	>600[d]	1190[d]	EFED[b]

[a] OPP/HED Toxicity Database

[b] OPP/EFED Toxicity Database

[c] cited in Johnson and Fagerstone 1994

[d] values for cholecalciferol have been adjusted, based on the purity of test material (30% ai); reported values for the 30% ai test material are LD50 >2000 mg/kg; northern bobwhite LC50 = 1744 (1233-2516); and mallard LC50 = 3926 (2631-9890)

Feeding studies: Several studies are available that provide additional information for characterizing hazards of rodenticide baits fed to birds. Some of these provide useful comparative information among different rodenticides tested under the same test protocol. For example, Lund (1981) fed 0.005% ai brodifacoum, 0.005% ai bromadiolone, and 0.025% ai warfarin baits to adult leghorn chickens (*Gallus gallus*). Two anticoagulants (coumatetralyl and difenacoum) not registered in the U. S. also were tested. Four hens per anticoagulant were individually presented with a choice of bait or untreated chicken food for up to 15 days; survivors were observed for an additional 2 weeks. All 4 hens fed brodifacoum bait died within 6 to 12 days (Table 6). Bromadiolone bait resulted in the deaths of 2 of 4 hens. No deaths or signs of toxicity occurred in 3 hens that ate warfarin bait (1 other hen refused to eat bait).

Christopher et al. (1984) also examined the hazards of several anticoagulant baits to 3-week-old leghorn chickens. Brodifacoum bait (0.005% ai) was given to 4 groups (6 chicks per group) on alternate days for 1, 2, 3, or 4 feedings. Bromadiolone bait (0.005% ai) was presented to 3 groups (6 chicks per group) on alternate days for 1, 2, or 3 feedings. Warfarin bait (0.025% ai) was fed to 2 groups (6 chicks per group) for either 3 or 21 consecutive days. Results are comparable to those reported by Lund (1981). Twelve (50%) of the 24 birds fed brodifacoum bait died (Table 7), whereas all birds survived after feeding on bromadiolone bait (18 birds) or warfarin bait (12 birds).

Two other studies provide additional information help on the hazard of brodifacoum bait to birds. Ross et al. (1979a,b) exposed 10 northern bobwhites and 10 ring-necked pheasants (*Phasianus colchicus*) to 0.005% brodifacoum pellets for 14 days. Six bobwhite and 6 pheasants died after feeding ad lib. on a choice of pellets or untreated food. ICI Americas, Inc. (1981) also reported deaths of several pheasants exposed to 50 ppm brodifacoum pellets broadcast in a pen study.

Two laboratory studies provide supplemental data on the primary hazard of warfarin to birds. Crabtree and Robison (1952) maintained chukar (*Alectoris chukar*) on a diet of warfarin bait for 30 consecutive days with no deaths. Jones and Townsend (1978; cited in Townsend et al.1981) reported no mortality of Japanese quail (*Coturnix coturnix*) fed 8 mg ai/kg/day of warfarin for 14 days.

Johnson and Fagerstone (1994) reviewed primary hazard information for zinc phosphide. They indicate that some birds are repelled by zinc phosphide and others may regurgitate bait. Spotted doves (*Streptopelia chinensis*), for example, reportedly regurgitated treated seeds about 1 hour after ingestion (Hilton et al. 1972, Pank et al. 1972). However, some laughing doves (*Streptopelia senegalensis*) died about 2 hours after eating treated bait, even though they had regurgitated bait about 20 minutes after ingestion (Siegfried 1968). In another study, 14 of 15 red-winged blackbirds (*Agelaius phoeniceus*) died after feeding for 48 hours on a 1:1 mixture of treated (2% ai) and untreated cracked corn (Schafer et al. 1970).

Table 6. Adverse Effects of Five Anticoagulant Baits Fed to Adult Leghorn Chickens for up to 15 Days (adapted from Lund 1981)

	Avg. intake per bird[a]			
Anticoagulant	bait (g)	ai (mg/kg)	Mortality	Adverse effects
Brodifacoum (0.005% ai)	362 (252-443)	10.5 (7.1-15.0)	4/4	death from day 6
Bromadiolone (0.005% ai)	496 (329-684)	12 (5.9-16.9)	2/4	loss of appetite; hemorrhage from day 6
Warfarin (0.025% ai)	922 (584-1232)	149 (132-171)	0/3	none
Coumatetralyl[b] (0.03% ai)	594 (313-820)	107 (79-137)	2/4	loss of appetite from day 8; hemorrhage
Difenacoum[b] (0.005% ai)	611 (458-835)	19 (13.5-28.3)	2/4	loss of appetite; hemorrhage from day 5

[a] range is given in parenthesis

[b] coumatetralyl and difenacoum are not registered in the U. S.

Table 7. Adverse Effects of Three Anticoagulant Baits Fed to 3-week-old Leghorn Chickens for 1 to 21 Days (adapted from Christopher et al. 1984)

Anticoagulant	No. feedings[a]	Avg. bait intake (g)	mg ai/kg	Mortality	Adverse effects
Brodifacoum (0.005% ai)	1	15.5	11.0	1/6	1 death on day 4;1 bird sick on day 12 but recovered
	2	30.0	21.0	1/6	1 death on day 7;1 bird sick on day 6 but recovered
	3	42.8	28.9	5/6	mortality from days 7-16; 1 bird sick on day 5 (sporadic bleeding) had not recovered by end of test (day 21)
	4	43.8	20.9	5/6	mortality from days 5-15; 1 bird sick on day 4 (sporadic bleeding) had not recovered by end of test (day 21)
Bromadiolone (0.005% ai)	1	13.2	12.1	0/6	none
	2	29.5	22.1	0/6	1 bird sick on day 17 but recovered
	3	13.2	36.9	0/6	1 bird sick on day 16 did not recover by end of test (day 21)
Warfarin (0.025% ai)	3	49.4	183.7	0/6	none
	21	305.3	1092.2	0/6	bleeding in 1 bird on days 12-16 but survived

[a] brodifacoum and bromadiolone baits were offered ad lib. on alternate days; warfarin bait was fed ad lib. for either 3 or 21 consecutive days

Other studies indicate that zinc phosphide bait poses a hazard to some birds, although some species may be less susceptible than others. Janda and Bosseova (1970) reported deaths of gray partridges that consumed as few as 6 to 9 treated (2.5% ai) wheat kernels, and ring-necked pheasants died after consuming as few as 18 to 25 kernels. The California Department of Fish and Game (CDFA 1962) reports that about 260 to 310 treated zinc phosphide grains (1% ai) provides an LD50 dose for geese, and a 5-lb goose is capable of ingesting as many as 6400 kernels in one feeding (Keith and O'Neill unpubl.; cited in Johnson and Fagerstone 1994). Ramey et al. (1994) exposed ring-necked pheasants and California quail (*Callipepla californica*) to 2% zinc phosphide bait in 0.2-ha alfalfa enclosures. Based on necropsy results, 16 (62%) of 26 pheasants died from consuming bait. None of the 26 California quail died. Glahn and Lamper (1983) exposed 12 Canada geese (*Branta canadensis*) and 12 white-fronted geese (*Anser albifrons*) to 1% zinc phosphide bait applied in hay cover crops in California. The geese, held in portable enclosures that were moved daily, were allowed to feed for 4 days. Four (33%) Canada geese died. All white-fronted geese survived, which the authors attributed to their developing an aversion to bait after ingesting sublethal doses during the first 2 days of exposure.

Avian reproduction/sublethal effects: No guideline data are currently available for any of the rodenticides. OPP will be requiring avian reproduction tests with the mallard and northern bobwhite to fulfill this guideline requirement (40 CFR §158.490 Wildlife and Aquatic Organisms Data Requirements, Guideline Reference No. 71-4). EFED notes that there is a published abstract reporting the deaths of 2 turkey vulture (*Cathartes aura*) offspring that were fed brodifacoum-poisoned mice by their parents (Borst et al. 2000). The possibility exists that young animals may be more susceptible to rodenticide poisoning than are adults (see also the section on "*Mammalian reproduction/sublethal effects*"). EFED will assess the potential for adverse reproductive and chronic effects when the guideline studies become available.

Mammals

Acute-oral and dietary toxicity: The available acute-oral and dietary toxicity data for mammals are presented in Tables 8, 9, and 10. Laboratory-rat or mouse LD50 values are used to calculate the amount of formulated bait and number of bait pellets that nontarget mammals of various sizes need to eat to ingest a dose lethal to 50% of the individuals in the population. Data for other species provide additional characterization of mammalian toxicity and indicate that rodenticides are not selective for the target species. Some dietary data also are available for the laboratory rat for 5 of the anticoagulants, and these data are used to calculate dietary RQs. Additionally, as previously noted, all registered rodenticide products have been tested under Agency guideline requirements and proven efficacious in killing target species.

Warfarin toxicity values deserve special mention. LD50 values for the laboratory rat vary markedly among warfarin studies in the EPA/EFED toxicity database, ranging from 2.5 to 680 mg/kg. Jackson and Ashton (1992) cite values ranging from 14 to 186 mg/kg and Hone and Mulligan (1982; cited in Buckle 1994) values from 1.5 to 323 mg/kg. According to Meehan (1984; cited in Buckle 1994), the most reliable estimates now place the LD50 for the Norway rat as somewhere between 10 and 20 mg/kg. Discrepancies might exist due to difference in strain and gender of the rats and in the carrier used to administer the dose. Poché and Mach (2001) also suggest that the degradation rate of warfarin in the gastrointestinal tract (GIT) of rats probably depends on the variation of bacterial species present and their abundance.

Table 8. Acute Oral Toxicity of Second-generation Anticoagulants to Mammals

Rodenticide/ Species	LD50, mg ai/kg (95% CI)	LC50, ppm (95% CI)	Reference
Brodifacoum			
Laboratory rat		0.53 (0.45-0.68) 0.55 (0.45-0.68) 0.55 (0.45-0.68) 0.57 (0.53-0.61) 0.85 (0.67-1.06)	EPA unpublished data[a]
Laboratory rat	0.41% (0.35-0.50) 0.56& (0.47-0.66)		EPA 1998a
Rat	0.39		HED[b]
Mouse	0.4		HED[b]
Vole	0.2 (0.11-0.32)	1.4 (0.77-2.0)	HED[b]
Richardson's ground squirrel	0.13 (0.06-0.19)		Baril and Pallister 1981[c]
Possum	0.17		Godfrey 1985
Pine vole	0.36 (0.22-0.59)		Byers 1978
Meadow vole	0.72 (0.53-0.98)		Byers 1978
Dog	0.25-1.0		HED[b]
Rabbit	0.29		HED[b]
Pig	<2.0		HED[b]
Guinea pig	2.7		HED[b]
Mink	9.2 (0-19.5)		Ringer and Aulerich 1978
Cat	~25		HED[b]
Sheep	>25		HED[b]

Rodenticide/ Species	LD50, mg ai/kg (95% CI)	LC50, ppm (95% CI)	Reference
Difethialone			
Laboratory rat	0.55 (0.53-0.57)		HED[b]
Rat	0.4-0.8		HED[b]
Laboratory mouse	1.29 (0.73-1.85)		HED[b]
Roof rat	0.38		Lorgue et al.[d]
House mouse	0.47		Lorgue et al.[d]
Norway rat (wild)	0.29-0.51		Lorgue et al.[d]
Hare	0.75		Lorgue et al.[d]
Pig	2-3		Lorgue et al.[d]
Dog	4		Harling et al. 1986[f]
Dog	11.8 (6.6-21.2)		HED[b]
Cat	>16		Lorgue 1986[e]
Bromadiolone			
Laboratory rat		0.92 (0.54-1.13) 1.49 (1.21-2.06) 1.79 (1.57-2.06) 1.99 (1.62-2.27)	EPA unpublished data[a]
Laboratory rat	0.56-0.84[f]		EPA 1998a
Laboratory mouse	1.75 (0.2-3.3)		HED[b]
Pine vole	3.9 (2.3-6.8)		Byers 1978
Rabbit	1		HED[b]
Dog	8.1		Poché 1988
Cat	>25		HED[b]

[a] the 5 dietary tests for brodifacoum and 4 dietary tests for bromadiolone were conducted at EPA's former Toxicology Unit, Beltsville, MD; methodology follows that described in McCann et al. 1981

[b] OPP/HED Toxicity Database

[c] cited in Matschke et al. 1983

[d] cited in Lechevin and Poché 1988

[e] cited in LiphaTech 1997

[f] an LD50 could not be statistically determined from the data but was estimated to be between these two test concentrations

Table 9. Acute Oral Toxicity of First-generation Anticoagulants to Mammals

Rodenticide/ Species	LD50, mg/kg (95% CI)	LC50, ppm (95% CI)	Reference
Chlorophacinone			
Laboratory rat		1.14 (1.02-1.36) 1.14 (0.98-1.35) 1.26 (1.11-1.47) 1.26 (0.97-1.64)	EPA unpublished data[a]
Laboratory rat	6.2 3.1% (1.5-6.7) 11.0& (6.5-18.5)		HED[b]
Laboratory rat	0.95 (5-day dose @ 0.19/day)		Jackson and Ashton 1992
Norway rat (wild)	0.80 (5-day dose @ 0.16/day)		Jackson and Ashton 1992
House mouse	1.0 6		Hone and Mulligan 1982[c]
Laboratory mouse	5.95 (5-day dose @ 1.19/day) 1.90% 17.40&		Jackson and Ashton 1992
Deer mouse	0.49		Clark 1994
Deer mouse	1.0-3.75[d]		Schafer and Bowles 1985
Norway rat	5.0		Clark 1994
Pine vole	14.2 (11.4-17.6)		Byers 1978
Roof rat	15.0		Clark 1994
Dog	50-100		Labe and Lorgue 1977
Diphacinone			
Laboratory rat		2.08 (1.57-2.76) 2.55 (1.79-3.19)	EPA unpublished data[a]
Laboratory rat	2.5% (1.3-3.4) 2.1& (1.5-2.9)		HED[b]
Laboratory rat	7.0 (5.2-9.5)		HED[b]
Laboratory rat	1.05 (5-day dose @ 0.21/day)		Jackson and Ashton 1992

Rodenticide/ Species	LD50, mg/kg (95% CI)	LC50, ppm (95% CI)	Reference
Norway rat (wild)	1.75 (5-day dose @ 0.35/day)		Jackson and Ashton 1992
Laboratory rat	1.9		Gaines 1969
House mouse	141-340		Hone and Mulligan 1982[c]
Laboratory mouse	7.05 (5-day dose @ 1.41/day) 2.10% 14.15&		Jackson and Ashton 1992
Meadow vole	14.0 (8.8-22.1)		Byers 1978
Pine vole	57.0 (34.4-94.3)		Byers 1978
Mongoose	0.2		EPA 1998a
Coyote	0.6		EPA 1998a
Dog	0.88		Kosmin and Barlow 1976[e]
Dog	3.0-7.5		Mount and Feldman 1983[e]
Dog	5-15		Lisella et al. 1971[e]
Cat	14.7		Clark 1994
Cat	5-15		Lisella et al. 1971[e]
Rabbit	35		Clark 1994
Warfarin			
Laboratory rat		4.41 (3.43-5.64) 5.43 (4.23-7.00) 5.91 (4.66-7.51) 6.03 (4.45-8.20)	EPA unpublished data[a]
Laboratory rat	2.5-5.0		WARF Institute 1977[f]
Laboratory rat	2.5-20		Til et al. 1974[f]
Laboratory rat	3		Gaines 1969
Laboratory rat	35.7% 41.9&		EPA 1982
Laboratory rat	323%[g] 58&[g]		Hagan and Radomski 1953[f]

Rodenticide/ Species	LD50, mg/kg (95% CI)	LC50, ppm (95% CI)	Reference
Laboratory rat	450-680% <10&		WARF Institute 1977[f]
Laboratory rat	100%[g] 8.7&[g]		Back et al. 1978[f]
Laboratory rat	1.65 (5-day dose @ 0.33/day)		Jackson and Ashton 1992
Norway rat (wild)	2.20 (5-day dose @ 0.44/day)		Jackson and Ashton 1992
Laboratory mouse	374[g]		Hagan and Radomski 1953[f]
Laboratory mouse	11.00 (5-day dose @ 2.20/day) 4.35% 40.00&		Jackson and Ashton 1992
Rabbit	800[g]		Hagan and Radomski 1953[f]
Cat	2.5-20		HED[a]
Dog	20-50		USFWS[h]
Dog	200-300[g]		Hagan and Radomski 1953[f]

[a] the 5 dietary tests for brodifacoum and 4 dietary tests for bromadiolone were conducted at EPA's former Toxicology Unit, Beltsville, MD; methodology follows that described in McCann et al. 1981

[b] OPP/HED Toxicity Database

[c] cited in Hyngstrom et al. 1994

[d] an approximate lethal dose (ALD); the ALD is estimated from an acute oral test that uses too few concentrations and test animals to statistically derive an LD50

[e] cited in LiphaTech 1997

[f] cited in EPA 1981

[g] values are for sodium warfarin

[h] cited in Papworth 1958

Table 10. Acute Oral Toxicity of non-Anticoagulant Rodenticides to Mammals

Rodenticide/ Species	LD50, mg ai/kg (95% CI)	Reference
Bromethalin		
Laboratory rat	10.7% 9.1&	HED[a]
Roof rat	6.6	Jackson et al. 1982
Mouse	5.3% 8.1&	HED[a]
Mouse	35.9% 28.9&	HED[a]
Rabbit	2.4% 2.0&	HED[a]
Dog	4.8	HED[a]
Cat	18	HED[a]
Zinc phosphide		
Norway rat (wild)	21 (13-34)	EPA 1998b
Rat	30 (20-45)	HED[a]
Rat	40	HED[a]
Roof rat	2.9-40	EPA 1998b
Polynesian rat	23	EPA 1998b
Deer mouse	40.5	Clark 1994
Deer mouse	42[b]	Schafer and Bowles 1985
Meadow vole	18	EPA 1998b
Nutria	5.5	EPA 1998b
Pocket gopher	6.8	EPA 1998b
Banner-tailed kangaroo rat	8	Clark 1994
Black-tailed prairie dog	18	EPA 1998b
Muskrat	29.9	Evans et al. 1966[c]
California ground squirrel	33.1	EPA 1998b
Black-tailed jack rabbit	8.2	EPA 1998b
Dog	40[b]	Matschke and LaVoie 1976[c]
Cat	40[b,c]	Matschke and LaVoie 1976[c]

Rodenticide/ Species	LD50, mg ai/kg (95% CI)	Reference
Kit fox	93 (62-140)	Schitoskey 1975
Cholecalciferol		
Laboratory mouse	26[d]	HED[a]
Laboratory rat	42 (33-53)[e]	HED[a]
Dog	88[e]	Marshall 1984

[a] OPP/HED Toxicity Database

[b] an approximate lethal dose (ALD); the ALD is estimated from an acute oral test that uses too few concentrations and test animals to statistically derive an LD50

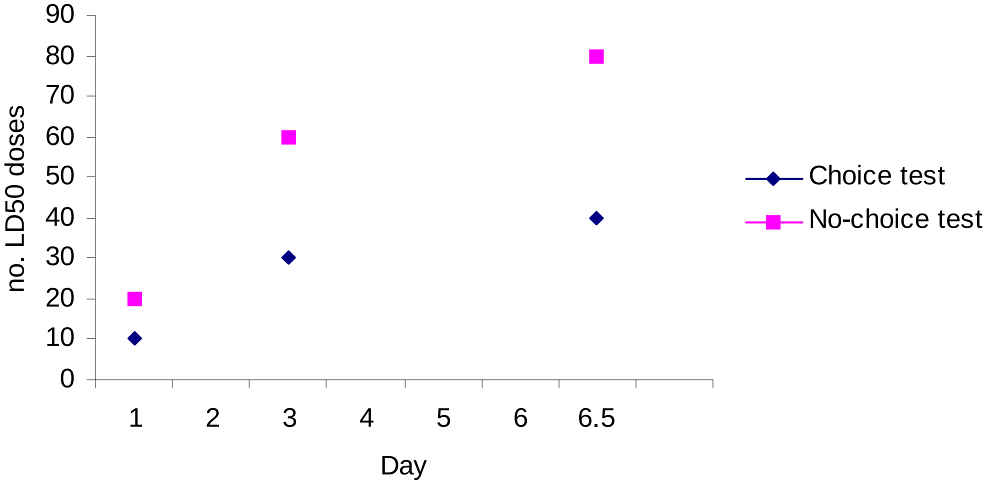
[c] cited in Johnson and Fagerstone 1994

[d] the value is adjusted, based on the purity of the test material (62.5%)

[e] the purity of the test material was not reported

Other toxicity information: ICI Americas, Inc. (1978b) provided some pertinent information on the approximate number of LD50 doses captive wild Norway rats consumed in their food (50 ppm brodifacoum bait) at various times until death, which averaged 6.5 days. The rats (sample size not specified) were either offered bait only or a choice of bait and untreated food. The rats in the no-choice group consumed an average of approximately 20 LD50 doses after 1 day of feeding and 80 LD50 doses by death (Figure 1). Rats offered a choice of bait or untreated food still consumed enough bait to have ingested an average of 40 LD50 doses at death.

Figure 1. Average number of LD50 doses consumed by captive wild Norway rats offered 50 ppm brodifacoum bait in no-choice (bait only) or choice (bait and untreated food) feeding tests (after ICI Americas, Inc. 1978b)



Some information is available to characterize the primary hazard of rodenticide bait to dogs and other nontarget species. Mackintosh et al. (1988) reported that some dogs have died after consuming as few as 8 brodifacoum (Talon) pellets. Lechevin and Poché (1988) indicate that 400 g of 0025% ai difethialone bait is the maximum amount tolerated by 10-kg dogs. In a study in which 2 dogs were exposed to a 0.025% ai warfarin bait, 1 died after feeding for 7 days on 12 g of bait daily and the other after feeding on 4.8 g of bait daily for 12 days (Prier and Derse 1962). Marsh (1985) calculated that an LD50 dose to a 10-lb dog could be provided with 23 g of brodifacoum bait, 85 g of diphacinone bait, 369 g of warfarin bait, and 1000 g of bromadiolone bait. Gunther et al. (1988) fed cholecalciferol bait to 4 dogs as a follow-up to an investigation of 2 dogs that died after consuming cholecalciferol bait. Two dogs were given a single meal containing approximately 540 g of bait (20 mg ai/kg) and 2 were given half that amount. All 4 dogs became lethargic, weak, and anorectic within 48 hours and all died 65 to 77 hours after treatment. These findings suggest that cholecalciferol bait may present more of a hazard to dogs than the LD50 of 88 mg ai/kg would suggest.

Dubock and Kaukeinen (1978) reported the following nontarget-hazards data for brodifacoum: "The deer mouse *Peromyscus maniculatus* completely succumbed (20/20 mortality) in a 1-day no-choice feeding test with 50 ppm brodifacoum (Marsh, unpublished)." and "100% mortality has been obtained against the ground squirrel *Spermophilus beecheyi* when offered 50 ppm brodifacoum bait no choice for 1, 2 or 3 days (Marsh, unpublished)."

Mammalian reproduction/sublethal effects: EFED typically utilizes the rat two-generation reproduction test to assess reproductive risks to mammals. This study (40 CFR §158.340 Toxicology Data Requirements, Guidelines Reference No. 83-4) is required by HED to support registration of pesticides with food uses or where use of the product is likely to result in human exposure over a significant portion of the human lifespan. This study is not currently available for any of the 9 rodenticides. HED also requires other subchronic/chronic studies, but most (e.g., dermal, inhalation, oncogenicity, neurotoxicity) provide measurement endpoints not relevant to assessing risk to nontarget mammals other than humans.

Some evidence exists that sublethal doses can have adverse effects. The Warfarin RED (EPA 1991a) notes that warfarin is a teratogen, and product labels are required to warn that "Exposure to warfarin during pregnancy should be avoided. Warfarin may cause harm to the fetus, including possible birth defects." The Rodenticide Cluster RED (EPA 1998a) reports developmental toxicity (e.g., vaginal bleeding, hypotonicity) in rats and rabbits exposed to bromadiolone at about two orders of magnitude less than the LD50 dose. In brodifacoum studies, internal hemorrhage and significantly prolonged prothrombin time of rabbits was reported for those dosed during gestation at about two orders of magnitude less than the LD50 dose. More recently, Munday and Thompson (2003) detected brodifacoum in two dog pups that died a few hours after birth. Of 13 pups from a single litter, eight were born dead or died within 48 hours of birth. Three puppies that died shortly after birth were necropsied. Two exhibited hemorrhage in the thoracic and peritoneal cavities, intestinal serosa, and meninges, and brodifacoum was detected in the liver of both puppies. The mother did not have any clinical signs of coagulopathy before or subsequent to whelping, and the authors suggest that fetuses may be more susceptible to brodifacoum than are adults.

Secondary-hazards Data

Birds

The available laboratory studies indicate that major differences occur among the rodenticides in their secondary hazard to birds, with brodifacoum displaying the greatest hazard and chlorophacinone and the non-anticoagulants the least. Thirty-one studies are cited in which raptors or avian scavengers were exposed to rodenticide in whole or ground carcasses, usually those of rats or mice, or in fortified meat. Second-generation anticoagulants were tested in 15 studies, first-generation-anticoagulants in 13 studies, and non-anticoagulants in 6 studies (note: some studies included more than one rodenticide group). Most prey animals were fed treated bait, although some were orally dosed. Most studies involved only 1 rodenticide but often more than 1 raptor or scavenger species was tested. Mortality is a measurement endpoint in all studies.

Some studies also report signs of toxicosis (e.g., bleeding, prolonged blood-coagulation time, abnormal behavior, regurgitation) in surviving test animals, and that information is included if reported. Although exposure scenarios, test species, and the number of test animals vary among the studies, collectively they provide sufficient information to characterize secondary hazards from short-term exposure. The studies are summarized and tabulated below. Two studies merit additional attention, because they test different rodenticides against the same test species under the same test conditions, and are discussed in more detail in the section "*Comparative anticoagulant studies*".

Second-generation anticoagulants: Some data are available for brodifacoum and bromadiolone but none for difethialone. Brodifacoum was tested in 11 studies involving 8 species. Of 149 individuals exposed to brodifacoum-poisoned prey, 63 (42%) individuals died (Table 11). Mortality occurred in 11 of 20 barn owls (*Tyto alba*), 6 of 6 red-tailed hawks (*Buteo jamaicensis*) and red-shouldered hawks (*Buteo lineatus*), 13 of 65 American kestrels (*Falco sparverius*), 1 of 4 Eurasian harriers (*Circus pygargus*), and 32 of 50 laughing gulls (*Larus atricilla*). No deaths occurred in 4 golden eagles (*Aquila chrysactos*) tested by Marsh and Howard (1978), but 3 bled externally. Some studies did not report whether signs of toxicosis were observed in surviving birds or not. In those studies that examined survivors for signs of toxicosis, such as external bleeding, internal hemorrhaging, and/or prolonged blood-coagulation time, about one-third of the survivors visually examined or necropsied exhibited symptoms of toxicity.

In contrast to brodifacoum, secondary exposure to bromadiolone caused the deaths of only 9 (8%) of 118 individuals in 5 studies (Table 12) that tested great-horned owls (*Bubo virginianus*), barn owls, red-tailed hawks, and Eurasian buzzards (*Buteo buteo*). Survivors also exhibited fewer signs of intoxication than did survivors in brodifacoum studies. Grolleau et al. (1989) reported bleeding in some of the 27 Eurasian buzzards that survived feeding on bromadiolone-poisoned voles for 3 days but reported no signs of intoxication in 59 survivors exposed for only 1 or 2 days. No signs of intoxication are reported by Poché (1988) or Mendenhall and Pank (1980) in 12 raptors (barn owls and red-tailed hawks) that survived feeding on bromadiolone-treated rodents for 3 to 10 days. Wyllie (1995) reported increased blood coagulation time in 6 barn owls fed bromadiolone-poisoned mice for 6 days, but coagulation times returned to normal within 10 days; all owls survived, and no evidence of hemorrhaging was seen.

Table 11. Secondary Hazards of Brodifacoum to Birds in Laboratory Studies

Predator/ scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of brodifacoum toxicity[a]	Reference
Barn owl	rats fed choice of 0.002% bait[b] and untreated food for 5 days	1-2	1	1	0	0	Mendenhall and Pank 1980
			3	2	2	no survivors	
			6	1	1	no survivors	
			8	2	2	no survivors	
Barn owl	mice fed 0.002% bait[b] for 1 day	3	1	6	4	nr	Newton et al. 1990 and Wyllie 1995
		2	3	2[c]	0	nr	
		2	6	2[c]	0	2 (eb/ct)	
Barn owl	mice fed 0.005% bait for 1-2 days	enough to provide 50-220 µg ai per day	15	4	1	3 (eb/ih)	Gray et al. 1994
Barn owl	rats fed 0.005% bait	4 total	5-7	4	1	0	Lee 1994[d]
Red-tailed hawk	rats fed 0.005% bait for 3 days	limited[e]	4	4	4	no survivors	Marsh and Howard 1978
Red-shouldered hawk	mice fed 0.005% bait for 3 days	limited[e]	4	2	2	no survivors	Marsh and Howard 1978
Golden eagle	rats fed 0.005% bait for 3 days	limited[e]	4	4	0	3 (eb)	Marsh and Howard 1978
American kestrel	voles fed 0.005% bait for 3 days	1	2	10	0		Savarie and LaVoie 1979
		1	6	10	4	(ct)	
American kestrel	ground vole tissue at 5 concentrations: 0.3 ppm	ad lib.	5	8	0	nr	LaVoie 1990
	0.8 ppm		5	8	1	nr	
	1.6 ppm		5	8	0	nr	
	3.2 ppm		5	8	0	nr	
	6.0 ppm		5	8	4	nr	

Predator/ scavenger (p/s)	Prey offered to p/s		No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of brodifacoum toxicity[a]	Reference
Eurasian buzzard	mice fed 0.005% bait		5	6	5	4	1 (bl)	Lutz 1987[d]
Australasian harrier	rabbit dosed at 6.5 mg ai/kg		1	1	4	1	nr	Godfrey 1985
Laughing gull	ground, spiked rat tissue at 5 concentrations:	0.72 ppm	ad lib.	5	5	3	0	ICI Americas, Inc. 1979a
		1.62 ppm		5	5	5	no survivors	
		3.41 ppm		5	5	5	no survivors	
		7.26 ppm		5	5	5	no survivors	
		14.0 ppm		5	5	5	no survivors	
Laughing gull	ground, spiked rat tissue at 5 concentrations:	0.13 ppm	ad lib.	5	5	0	0	ICI Americas, Inc. 1979b
		0.34 ppm		5	5	1	0	
		0.84 ppm		5	5	0	1 (eb)	
		2.10 ppm		5	5	4	0	
		5.26 ppm		5	5	4	0	

[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

[a] registered baits are 0.005% ai

[c] the 2 owls that survived the initial 1-day exposure were subsequently re-exposed for 3 days and again for 6 days; the owls were allowed to recover for 75 to 79 days between exposure periods

[d] cited in Joermann 1998

[e] the amount of food offered to the raptors was "limited" to prevent overindulgence on any given day

Table 12. Secondary Hazards of Bromadiolone to Birds in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of bromadiolone toxicity[a]	Reference
Barn owl	rats fed choice of 0.005% bait or untreated food for 5 days	1-2	1	1	0	0	Mendenhall and Pank 1980
			3	2	0	0	
			6	1	0	0	
			10	2	1	0	
Barn owl	mice fed commercial bait (% ai not reported) and allowed to die	2-3	6	6	0	(ct)[c]	Wyllie 1995
Barn owl	rats fed 0.005% bait	4	5-7	4	1	nr	Lee 1994[d]
Eurasian buzzard	voles fed 0.01% bait[b]	1	1	40	0	0	Grolleau et al. 1989[d]
			1+1[e]	10	1	0	
			2	10	0	0	
			3	30	2	some (bl)	
Eurasian buzzard	mice fed 0.005% bait	?	10	4	3	1 (ct)	Lutz 1986[d]

[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

[b] rat and mouse baits registered in the U. S. are 0.005% ai

[c] coagulation time returned to normal within 10 days; no signs of hemorrhage in any individuals

[d] cited in Joermann 1998

[e] a second 1-day exposure period occurred 10 days after the first exposure

Only a few studies provide information on the residue level in the prey species offered to the secondary consumer. In those studies, the experimenter often manipulated residue levels to provide a known concentration or range of concentrations (e.g., ICI Americas, Inc. 1979a,b; LaVoie 1990; Gray et al. 1994). Additional information on whole-body residues in target species exposed to second-generation anticoagulants is provided in Table 13. Note that animals collected in the field were exposed to bait for an undetermined number of days. Some laboratory studies used bait concentrations different from that in baits registered in the U. S. and some exposed the primary consumer for only 1 day (e.g., Newton et al. 1990, Poché 1988).

Two residue studies indicate that the amount of whole-body residue in the target species is related to the amount of active ingredient in the bait. Kaukeinen (1982) provides mean tissue residue levels in voles exposed to brodifacoum bait in the laboratory. Separate groups of males and females were exposed for 4 days to 50 ppm bait or 10 ppm bait. Residues are 5.21 ppm and 2.17 ppm for males and females, respectively, exposed to 50 ppm bait but only 0.53 ppm and 0.40 ppm, respectively, for those exposed to 10 ppm bait. In field trials for vole control in orchards, Merson et al. (1984) collected voles 1 to 7 days after bait application. Two collections of voles exposed to 0.005% ai bait had mean whole-body residues of 2.07 ppm and 4.07 ppm, whereas those exposed to 0.001% ai bait had a mean residue level of 0.35 ppm.

Table 13. Second-generation Anticoagulant Residue Levels in Primary Consumers

Rodenticide	mg ai/kg bait	Target species	Site	Sample size	Days exposed	Whole-carcass residue (ppm)	Reference
Brodifacoum	50	rat	field	50	unknown	most <7; some up to 11-13	Kaukeinen 1993
Brodifacoum	50	rat	field	6	unknown	2.7 (0.1-6.6)	ICI 1979c
Brodifacoum	50	rat	field	4 % 3 & 3 juv.	unknown	7.08 (3.92-9.17) 5.61 (1.39-12.19) 8.63 (1.77-25.97)	Howald 1997
Brodifacoum	50	vole	field	74	1-7	4.07 ± 0.20 (SE)	Merson et al. 1984
Brodifacoum	50	vole	field	62	1-7	2.07 ± 0.17 (SE)	Merson et al. 1984
Brodifacoum	50	vole	laboratory	15 % 15 &	4 4	5.21 ± 2.06 (sd) 2.17 ± 1.17 (sd)	Kaukeinen 1982
Brodifacoum	25[a]	deer mouse	field	10	4-9	2.71 (0.68-4.25)	Howald et al. 2001
Brodifacoum	20[a]	mouse	laboratory	?	3	2.21	Anonymous 1981[b]
Brodifacoum	20[a]	mouse	laboratory	10	1	0.44	Newton et al. 1990
Brodifacoum	10[a]	vole	laboratory	15 % 15 &	4 4	0.53 ± 0.24 (sd) 0.40 ± 0.20 (sd)	Kaukeinen 1982
Brodifacoum	10[a]	vole	field	43	1-7	0.35 ± 0.03 (SE)	Merson et al. 1984
Difethialone	25	rat	laboratory	20	3	2.0 ± 0.51(sd)	Goldade et al. 2001
Bromadiolone	50	rat	laboratory	6	1	2.08	Poché 1988
Bromadiolone	50	mouse	laboratory	10	1	2.29	Poché 1988
Bromadiolone	50	rat	field	16	unknown	1.92	Poché 1988
Bromadiolone	50	mouse	field	6	unknown	1.17	Poché 1988

Rodenticide	mg ai/kg bait	Target species	Site	Sample size	Days exposed	Whole-carcass residue (ppm)	Reference
Bromadiolone	50	ground squirrel	field	16	unknown	0.49	Poché 1988
Bromadiolone	100[a]	vole	laboratory	?	1	6.5-6.75	Grolleau et al. 1989
Bromadiolone	100[a]	vole	laboratory	?	3	8.7-10.9	Grolleau et al. 1989
Bromadiolone	100[a]	vole	laboratory	?	3	5.8	Grolleau et al. 1989
Bromadiolone	150[a]	vole	field	44	$\leq$3	0.91 (0.05-2.97)	Delley and Joseph 1985[c]
Bromadiolone	150[a]	vole	laboratory	12	$\leq$3	0.11 (0.04-0.19)	Delley and Joseph 1985[c]

[a] brodifacoum and bromadiolone baits registered in the U. S. are 0.005% ai
[b] cited in Joermann 1998
[c] cited in Saucy et al. (2001)

First-generation anticoagulants: Mortality in studies with the 3 first-generation anticoagulants ranged from 0 to 9%. No mortality occurred in 8 chlorophacinone studies with 112 individuals from 9 species (Table 14). Birds tested included 28 carrion crows (*Corvus corone*), 20 Eurasian buzzards, 20 American kestrels, 20 black-billed magpies, 10 red-tailed hawks, 6 white storks (*Ciconia ciconia*), 4 tawny owls (*Strix aluco*), 2 barn owls, and 2 great horned owls. Some survivors showed signs of intoxication, mostly prolonged blood-coagulation time. About 9% mortality was recorded in 3 diphacinone studies with 34 individuals (Table 15). Test species were barn owls, great horned owls, saw-whet owls (*Aegolius acadicus*), golden eagles, and American crows (*Corvus brachyrhynchos*). Thirteen (42%) of the survivors displayed some signs of toxicity. In 4 warfarin studies, 2 (9%) of 23 individuals died (Table 16); no adverse signs were reported in the survivors. Whole-body residues in target species exposed to chlorophacinone, diphacinone, and warfarin are presented in Table 17.

Table 14. Secondary Hazards of Chlorophacinone to Birds in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of chlorophacinone toxicity[a]	Reference
Barn owl	rats fed choice of 0.005% bait or untreated bait for 5 days	1-2	10	2	0	0	Mendenhall and Pank 1980
Black-billed magpie	rats fed 0.005% bait for 5 days	ad lib.	5	20	0	0	Baroch 1997
American kestrel	voles fed 0.01% bait until dead	1	21	10	0	10 (eb/ih)	Radvanyi et al. 1988
		1 every 3 days	61	10	0	10 (eb/ih)	
Red-tailed hawk	voles fed 10 g 0.005% bait daily for up to 9 days	2	6	5	0	0	Askham and Poché 1992
Great horned owl	voles fed 10 g 0.005% bait daily for up to 9 days	2	6	1	0	0	Askham and Poché 1992
Red-tailed hawk	voles fed 0.005% bait for up to 9 days	2	6	5	0	0	Askham 1988
Great horned owl	voles fed 0.005% bait for up to 9 days	2	6	1	0	0	Askham 1988
Tawny owl	mice fed 0.0075% bait[b]	ad lib.	10	4	0	(ct)	Riedel et al. 1991[c]
Eurasian buzzard	mice fed 0.0075% bait[b]	ad lib.	7	4	0	(ct)	Riedel et al. 1991[c]
			10	6	0	(ct)	
			5+5+5[d]	3	0	(ct)	
			40	3	0	(ct)	
Eurasian buzzard	mice fed 0.0075% bait[b]	4	7	4	0	0	Anonymous 1978[c]
Carrion crow	mice fed 0.0075% bait[b]	ad lib.	10	4	0	(ct)	Riedel et al. 1991[c]
Carrion crow	mice fed 0.0075% bait[b]	3-4	3	12	0	0	Sterner 1978[c]
			5	12	0	0	

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of chlorophacinone toxicity[a]	Reference
White stork	mice fed 0.0075% bait[b]	ad lib. (treated /untreated)	3	3	0	1 or 2 (ct)	Sterner 1981[c]
			14	3	0	1 or 2 (ct)	

[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

[b] baits registered in the U.S. are either 0.005% or 0.01% ai

[c] cited in Joermann 1998

[d] the 3 5-day treatment periods are separated by 3 days when the birds were fed untreated mice

Table 15. Secondary Hazards of Diphacinone to Birds in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of diphacinone toxicity[a]	Reference
Great horned owl	mice fed choice of 0.01% bait or untreated food for 10 days	2	5	3	2	1 (ct)	Mendenhall and Pank 1980
Saw-whet owl	mice fed choice of 0.01% bait or untreated food for 10 days	2	5	1	1	no survivors	Mendenhall and Pank 1980
Barn owl	rats fed choice of 0.005% bait or untreated food for 5 days	ad lib.	10	2	0	0	Mendenhall and Pank 1980
American crow	rats fed 0.005% bait until death	1	1	10	0	0	Massey et al. 1997
		1-2[b]	6	11	0	5 (eb/ct)	
Golden eagle	meat laced at 2.7 ppm ai	454 g	5	4	0	4 (eb/ct)	Savarie et al. 1979
			10	3	0	3 (eb/ct)[c]	

[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

[b] offered 1 rat per crow for 5 days and 2 rats per crow on day 6

[c] general weakness of all eagles was observed after 5 days

Table 16. Secondary Hazards of Warfarin to Birds in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of warfarin toxicity[a]	Reference
Tawny owl	mice fed bait for 3 days	1 every other day	90	4	0	0	Townsend et al. 1981
			28	2[c]	0	0	
Black-billed magpie	rats fed 0.05% bait[b] for 4-7 days	ad lib.	5	14	0	0	March 1997
Barn owl	rats fed 0.005% bait[b]	4 total	5-7	4	2	nr	Lee 1994[d]
Eurasian buzzard	rat/mouse	ad lib.	18	1	0	nr	Telle 1955[d]

[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

[b] rat and mouse baits registered in the U.S. are 0.025% ai

[c] the 2 owls had previously been exposed for 90 days; untreated mice were offered for 3 weeks preceding the second test

[d] cited in Joermann 1998

Table 17. First-generation Anticoagulant Residue Levels in Primary Consumers

Rodenticide	mg ai/kg bait	Target species	Site	Sample size	Days exposed	Whole-carcass residue (ppm)	Reference
Chlorophacinone	100	ground squirrel	field	10	unknown	1.27 ± 0.56 (sd)	Baroch 1996b
Chlorophacinone	75[b]	mouse	laboratory	?	3	6.0	Riedel et al. 1991[a]
Chlorophacinone	50	ground squirrel	field	10	unknown	0.57 ± 0.27 (sd)	Baroch 1996a
Chlorophacinone	50	ground squirrel	field	10	unknown	0.52 + 0.31(sd)	Baroch 1996b
Chlorophacinone	50	rat	laboratory	5	5	0.47 (0.21-0.93)	Baroch 1997
Chlorophacinone	50	rat	laboratory	4	5	0.45 (0.18-0.81)	Ahmed et al. 1996
Chlorophacinone	50	vole	laboratory	10	≤9	3.2	Askham and Poché 1992
Chlorophacinone	50 or 100[c]	ground squirrel	field	62	unknown	0.264	Primus et al. 2001
Chlorophacinone	50 or 100[c]	vole	field	3	unknown	1.58 (0.26-4.1)	Primus et al. 2001
Chlorophacinone	50	mouse	laboratory	?	3	5.8	Anonymous 1981[a]
Chlorophacinone	50 or 100[c]	pocket gopher	field	8	unknown	0.518	Primus et al. 2001
Chlorophacinone	50 and 100[d]	ground squirrel	field	53	unknown	0.93	Goodall et al. 2002
Diphacinone	50	ground squirrel	field	10	unknown	1.4 (0.6-3.4)	Baroch 1994a
Diphacinone	50	ground squirrel	field	7	unknown	0.9 (0.48-1.89)	Baroch 1994b
Diphacinone	100	ground squirrel	field	10	unknown	1.4 (0.6-2.6)	Baroch 1994a
Diphacinone	50 and 100[d]	ground squirrel	field	76	unknown	0.98	Goodall et al. 2002
Warfarin	200[e]	mouse	laboratory	17	3	2.95 ± 0.26 (SE)	Townsend et al. 1984
Warfarin	67[e]	rabbit	laboratory	nr	35	104	Aulerich et al. 1987
Warfarin	50[e]	mouse	laboratory	62	3	1.63 ± 0.1 (SE)	Townsend et al. 1981

Rodenticide	mg ai/kg bait	Target species	Site	Sample size	Days exposed	Whole-carcass residue (ppm)	Reference
Warfarin	50[e]	mouse	laboratory	18	3	1.58 ± 0.1 (SE)	Townsend et al. 1984
Warfarin	25[e]	rabbit	laboratory	nr	35	82	Aulerich et al. 1987
Warfarin	10[e]	mouse	laboratory	15	3	0.42 ± 0.04 (SE)	Townsend et al. 1984

[a] cited in Joermann 1998

[b] chlorophacinone baits registered in the U. S. are either 0.005% or 0.01% ai

[c] carcasses were collected in the field in CA, where both 50 ppm and 100 ppm chlorophacinone baits are registered

[d] the study did not allow distinguishing among ground squirrels exposed to 50 ppm and 100 ppm baits

[e] warfarin baits registered in the U. S. are 0.025% ai

Comparative anticoagulant studies: Some of the most meaningful studies for comparing hazards are those in which more than one rodenticide was tested by the same researchers under the same test conditions and with the same test species. Any adverse effects observed can more readily be attributed to differences among the rodenticides than to differences potentially confounded from utilizing different exposure scenarios or test species. The 2 studies summarized below indicate that brodifacoum has greater secondary toxicity to birds than do other anticoagulants tested, including bromadiolone, difenacoum and flocoumafen (both second-generation anticoagulants not registered in the U. S.), diphacinone, chlorophacinone, and fumarin (a first-generation compound no longer registered in the U.S.).

Mendenhall and Pank (1980) compared secondary hazards of 3 second-generation and 3 first-generation anticoagulants to barn owls. Six owls per rodenticide were exposed for either 1, 3, 6, or 10 days to rats fed with either brodifacoum (20 ppm bait), bromadiolone (50 ppm bait), or difenacoum (50 ppm). The exposed rats had been offered free choice of bait (5 to 13 g daily) or laboratory chow for 10 days; thus, none were forced to eat bait. An additional 2 owls per rodenticide were exposed for 10 days to rats fed with either diphacinone (50 ppm), chlorophacinone (50 ppm), or fumarin (250 ppm). Six of the 18 owls exposed to second-generation anticoagulants died, whereas none of the 6 owls offered first-generation anticoagulant-poisoned rats exhibited any signs of intoxication. Brodifacoum-fed rats accounted for 5 of the 6 owl deaths, even though the concentration of active ingredient in the bait fed to the rats is less than the 50 ppm in baits registered for rat and mouse control. The other mortality occurred in 1 of 2 owls exposed to bromadiolone-fed rats for 10 days. The amount of anticoagulant residue in the rats offered to the owls was not determined.

Wyllie (1995) and Newton et al. (1990) reported on toxic effects to barn owls fed mice exposed to brodifacoum (6 owls), bromadiolone (6 owls), or 2 other anticoagulants (difenacoum, flocoumafen). The mice had been fed bait (no choice) for a single day and allowed to die, which took 2 to 11 days. Dead mice were then offered to the owls in 3 phases, each phase separated by a recovery period lasting at least 75 days. In phase I, each owl was offered 3 mice for 1 day only. Surviving owls were offered 6 mice each during a 3-day period in phase II and 12 mice each during a 6-day period in phase III. Mortality, evidence of external bleeding, and delays in blood-coagulation times were monitored. Four of the 6 owls fed brodifacoum-exposed mice died within 6 to 17 days of phase I. Both survivors also survived feeding on poisoned mice in phases II and III, but both exhibited bleeding from the mouth, feet, and newly-grown feathers for up to 30 days, and blood-coagulation times did not reach normal until 16 to 78 days after treatment. In contrast, none of the owls exposed to bromadiolone-poisoned mice died or exhibited signs of hemorrhaging, and blood coagulation times returned to normal 4 to 6 days after treatment.

Others (non-anticoagulants): The few studies available for the non-anticoagulant rodenticides indicate few adverse secondary effects. Five studies are available for zinc phosphide (Table 18). Test birds included 2 great horned owls, 3 spotted eagle owls (*Bubo africanus*), 3 kestrels (*Falco tinnunculus*), 3 bald eagles (*Haliaeetus leucocephalus*), 3 black vultures (*Coragyps atratus*), 3 carrion crows, a magpie, and a jay. None of the 19 birds died, but signs of intoxication were noted in several individuals. Roosting-behavior irregularities were noted in 2 owls exposed to poisoned voles for 3 days (Bell and Dimmick 1975), and 3 bald eagles fed poisoned nutria (*Myocastor coypus*) for 4 to 5 weeks regurgitated some prey (Evans et al. 1966; cited in Johnson and Fagerstone 1994). In the only study available for cholecalciferol (Table 19), no adverse effects were observed in 2 turkey vultures and 1 red-tailed hawk exposed to rats fed for 1-day with 0.075% ai bait (Marsh and Koehler 1991). Each bird was offered 1 large or 2 small rats daily for 10 days. No hazard data are available for bromethalin.

Some whole-body residue data are available for zinc phosphide but none was found for cholecalciferol or bromethalin. Sterner et al. (1998) reported a mean whole-body residue of 0.42 (± 0.68) mg ai per vole for 6 voles each offered 5 oat-groat particles treated with 2% zinc phosphide. Mean particle weight was 23 mg, resulting in individual voles being offered only about 0.12 g of bait. In an earlier study (Sterner and Maudlin 1995), whole-body residues averaged 1.73 mg ai per vole (range = 0.31 to 4.95 mg ai) in voles offered bait ad libitum. Almost all zinc phosphide detected in carcasses apparently was in undigested bait in the GIT. Matscke and Andrews (1990) recovered only 8.9% of the amount of 2% ai bait ingested by voles, and 99.9% of that was in the GIT, especially the stomach. Only 0.1% of that recovered was detected in the kidneys, gall bladder, liver, and spleen combined, and none was detected in the lungs, heart, or in muscle. Tkadlec and Rychnovsky (1990) also reported that 99% of the zinc phosphide residue they detected in voles was in the GIT.

Table 18. Secondary Hazards of Zinc Phosphide to Birds in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey of red daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of zinc phosphide toxicity	Reference
Great horned owl	voles fed bait (86.94 mg ai/kg)	ad lib.	3	2	0	2[a]	Bell and Dimmick 1975
Spotted eagle owl	gerbils fed 3-4 treated kernels (2% ai)	1	5 10 40	1 1 1	0 0 0	0 0 0	Siegfried 1968[b]
Kestrel	voles fed 5% bait[c]	1	3	3	0	0	Tkadlec and Rychnovsky 1990
Bald eagle	nutria fed 275 g bait (% ai not reported)	13-28 total per bird	28-35	3	0	3[d]	Evans et al. 1966[e]
Black vulture	nutria fed bait (% ai not reported)	not reported	10-11	3	0	0	Evans et al. 1966[e]
Carrion crow	mice fed 2.5% bait[c]	2-4	7	3	0	0	Anonymous 1980[b]
Magpie	mice fed 2.5% bait[c]	2-4	7	1	0	0	Anonymous 1980[b]
Jay	mice fed 2.5% bait[c]	2-4	7	1	0	0	Anonymous 1980[b]

[a] irregular roosting behavior was reported
[b] cited in Joermann 1998
[c] baits registered in the U. S. are 2% ai
[d] regurgitated prey
[e] cited in Johnson and Fagerstone 1994

Table 19. Secondary Hazards of Cholecalciferol to Birds in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of cholecalciferol toxicity[a]	Reference
Turkey vulture	rats fed 0.075% ai bait for 1 day	1 large or 2 small	10	2	0	0	Marsh and Koehler 1991
Red-tailed hawk	rats fed 0.075% ai bait for 1 day	1 large or 2 small	10	1	0	0	Marsh and Koehler 1991

Mammals

Laboratory tests indicate that the second-generation anticoagulants, as well as chlorophacinone and diphacinone, present a hazard to mammalian predators and scavengers. Thirty-three studies were found in which mammalian predators or scavengers were exposed to rodenticide in whole or ground carcasses, usually rats or mice, or in spiked meat. Second-generation anticoagulants were tested in 8 studies, first-generation-anticoagulants in 15 studies, and non-anticoagulants, mainly zinc phosphide, in 13 studies. Collectively, these studies provide sufficient information to characterize short-term secondary hazards for most of the rodenticides. Three studies in which different rodenticides were tested against the same test species under the same test conditions are discussed in more detail in the section *"Comparative anticoagulant studies*".

Second-generation anticoagulants: Mortality of 8 (42%) of 19 individuals (foxes, mustelids, domestic dogs) occurred in 4 brodifacoum studies (Table 20). Test subjects included 5 red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*), 4 mongooses (*Herpestes auropunctatus*), 4 weasels (*Mustela* sp.), and 6 domestic dogs. Signs of toxicity are reported for most survivors. In 4 bromadiolone studies (Table 21), 6 (23%) of 26 test animals died, including coyotes (*Canis latrans*), mongooses, and an ermine (*Mustela erminea*). Bleeding was observed in all 10 ermine that survived being fed 1 bromadiolone treated vole per day for 3 to 5 days, but not in 5 coyotes or 4 stone martens fed treated ground squirrels or mice for periods ranging from 1 to 5 days. No comparable secondary-hazard studies are available for difethialone. Goldade et al. (2001) estimated a chronic LD50 for European ferrets (*Mustela putorius furo*) fed difethialone-fortified dog food at various concentrations. The chronic LD50 of 760 mg ai/kg was estimated from cumulative daily food intake, difethialone concentration, and individual bird body weights, but only 2 ferrets were exposed to each test concentration and the duration of exposure was not specified.

First-generation anticoagulants: Laboratory studies indicate that chlorophacinone and diphacinone present a hazard to mammalian predators and scavengers. In 8 chlorophacinone studies, 32 (58%) of 55 individuals died, including 7 of 8 mongooses, 3 of 7 coyotes, 1 of 4 red foxes, 18 of 35 ferrets, and 3 of 4 weasels (Table 22). In 3 diphacinone studies, 19 (58%) of 33 test animals died after feeding on rodents fed diphacinone, liver tissue from owls fed diphacinone, or fortified meat. Species affected included mink (*Mustela vison*), mongooses, ermine, deer mice, rats, and dogs (Table 23). Warfarin appears to be less hazardous than other anticoagulants. In 7 studies, only 9 (9%) of 100 individuals died after eating warfarin-treated rodents (Table 24). Dead animals included 3 mink, 3 least weasels (*Mustela nivalis*), and 3 dogs.

Table 20. Secondary Hazards of Brodifacoum to Mammals in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of brodifacoum toxicity[a]	Reference
Red fox and Gray fox	rats dosed at 15 mg ai/kg[b]	400 g	1	2	0	2 (eb/ih)	ICI Americas, Inc. 1978a
			3	1	1	no survivors	
			4	2	1	1 (eb/ih)	
Mongoose	rats fed 0.002% bait[c] for 5 days	1	1	1	0	nr	Pank and Hirata 1976
			3	1	1	no survivors	
			6	1	0	nr	
			10	1	0	nr	
Weasel	mice fed 0.002% bait[c]	ad lib.	16-52	4	4	no survivors	Anonymous 1981[d]
Dog (domestic)	rats dosed at 15 mg ai/kg[b]	650 g	1-4	6	1	4 (eb/ih)	ICI Americas, Inc. 1978b

[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

[b] the rats were dosed to simulate feeding on 0.005% bait

[c] registered baits are 0.005% ai

[d] cited in Joermann (1998)

Table 21. Secondary Hazards of Bromadiolone to Mammals in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of bromadiolone toxicity[a]	Reference
Mongoose	rats fed 0.005% bait for 5 days	1	1	1	0	nr	Pank and Hirata 1976
			3	1	1		
			5	1	1		
			6	1	1		
Coyote	ground squirrels fed 15 g of 0.01% bait[b] for 3 days	1	5	7	2	0[c]	Marsh and Howard 1986
Ermine	voles fed 0.01% bait[b]	1	3	8	0	8 (bl)	Grolleau et al. 1989[d]
			5	3	1	2 (bl)	
Stone marten	mice fed 0.005% bait	8	1	2	0	0	Lund and Rasmussen 1986[d]
			4	2	0	0	

[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

[b] rat and mouse baits registered in the U. S. are 0.005% ai

[c] 2 coyotes stopped feeding for 8 and 16 days, which was attributed to bromadiolone intoxication; both resumed feeding and survived

[d] cited in Joermann 1998

Table 22. Secondary Hazards of Chlorophacinone to Mammals in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of chlorophacinone toxicity[a]	Reference
Mongoose	rats fed 0.005% bait for 5 days	1	1	1	0	nr	Pank and Hirata 1976
			3	1	1	no survivors	
			5	2	2	no survivors	
			6	1	1	no survivors	
			7	1	1	no survivors	
			9	1	1	no survivors	
			10	1	1	no survivors	
Coyote	ground squirrels fed 15 g of 0.01% bait for 6 days[b]	1	5	7	3	0	Marsh and Howard 1986
Red fox	mice fed 0.0075% bait[c]	20 total	4	1	1[d]	no survivors	Bachhuber and Beck 1988[e]
European ferret	rats fed 0.005% bait for 5 days	ad lib.	5	20	11	nr	Ahmed et al. 1996
European ferret	prairie dogs fed 25 g of 0.0025% bait daily for 6 days[c]	4 (1 every other day)	8	6	5	nr	Fisher and Timm 1987
European ferret	voles/mice fed 0.0075% bait[c]	5 total	4	2	1[f]	(ct)	Bachhuber and Beck 1988[e]
European ferret	muskrats fed 0.005% bait	ad lib.	4	2	0	1 (bl)	Jobsen 1978[e]
			8	1	1	no survivors	
European ferret	voles fed 0.0075% bait[c]	ad lib.	3	4	0	(ct)	Anonymous 1983[e]
Weasel	mice fed 0.005% bait	ad lib.	90	4	3	0	Anonymous 1981[e]

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[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

[b] ground squirrels were fed no-choice for 3 days followed by 3 days in which they had a choice of bait or untreated laboratory chow

[c] baits registered in the U.S. are either 0.005% or 0.01% ai

[d] individual was sacrificed but considered 'dead' based on coagulation index

[e] cited in Joermann 1998

[f] individual recovered from moribund state after administration of antidote, but assumed 'dead' without antidote treatment

Table 23. Secondary Hazards of Diphacinone to Mammals in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of diphacinone toxicity[a]	Reference
Mink	nutria fed 0.01% carrot bait for up to 10 days	ad lib.	5-18	3	3	no survivors	Evans and Ward 1967
Mongoose	rats fed 0.005% bait for 5 days	1	1	1	0	nr	Pank and Hirata 1976
			3	1	1	no survivors	
			5	2	2	no survivors	
			6	1	1	no survivors	
			7	1	1	no survivors	
			8	1	1	no survivors	
			10	1	1	no survivors	
Ermine	deer mice fed 0.01% bait for 10 days	2	5	2	1	nr	Pank and Hirata 1976
Striped skunk	deer mice fed 0.01% bait for 10 days	2	5	5	0	nr	Pank and Hirata 1976
Deer mouse	liver from diphacinone-poisoned owls	1 g daily	7	4	1	3 (ct)	Pank and Hirata 1976
Rat	meat containing 0.5 ppm ai	ad lib.	6	8	4	nr	Savarie et al. 1979
Dog (domestic)	nutria fed 0.01% carrot bait for up to 10 days	ad lib.	6-10	3	3	no survivors	Evans and Ward 1967

[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

Table 24. Secondary Hazards of Warfarin to Mammals in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of warfarin toxicity[a]	Reference
Mink	nutria fed 0.025% bait for at least 7 days	ad lib.	8-15	3	3	no survivors	Evans and Ward 1967
Mink	rabbits fed 25 or 67 ppm ai bait[b] for 5 weeks	ad lib.	28	50	0	0	Aulerich et al. 1987
Least weasel	mice fed 0.001% bait,	ad lib.	90	2	0	2 (ct)	Townsend et al. 1984
	0.005% bait,		29-90	2	1	1 (ct)	
	or 0.02% bait for 3 days		12-57	2	2	no survivors	
European ferret	prairie dogs fed 0.05% bait[b] for 15 days	1	7	10	0	0	Carlet and Mach 1997
European ferret	prairie dogs fed 0.05% bait[b] for 5 days	ad lib.	5	10	0	0	Mach 1998
Raccoon	rats fed 0.025% bait for 5 days	1	5	8	0	0	EPA 1982
		3	5	10[c]	0	0	
Dog (domestic)	nutria fed 0.025% bait for at least 7 days	ad lib.	8-16	3	1	2 (eb/ct)	Evans and Ward 1967
Dog (domestic)	mice fed 0.025% bait,	4-10	56	4	0	0	Prier and Derse 1962
	0.05% bait;	10	56	1	0	0	
	mice dosed with 2.5 mg ai;	1	56	1	0	0	
	10 mg ai;	1	25	1	1	no survivors	
	40 mg ai	1	17	1	1	no survivors	

[a] eb = external bleeding; ih = internal hematoma; bl = bleeding (unspecified); ct = increased blood coagulation time; nr = not reported

[b] registered baits are 0.025% ai

[c] the 10 test animals included the 8 individuals from the first trial plus 2 additional untested individuals

Comparative anticoagulant studies: Marsh and Howard (1986) conducted a pen study to determine if ground squirrels fed either bromadiolone or chlorophacinone pose a secondary hazard to coyotes. The ground squirrels were fed either 0.01% ai bromadiolone bait or 0.01% ai chlorophacinone bait for 5 consecutive days. Each coyote (7 per rodenticide) was offered 1 dead ground squirrel per day for 5 days and observed for 30 days posttreatment. Three coyotes died after feeding on the dead ground squirrels previously fed chlorophacinone. All 7 coyotes fed dead ground squirrels previously fed bromadialone survived, although 2 consumed very little of their normal food rations for 8 to 16 days after treatment.

Pank and Hirata (1976) fed poisoned rats to mongooses to examine possible secondary hazards of anticoagulant rodenticides. The rats were fed for 5 days with baits that included 0.002% ai brodifacoum, 0.005% ai bromadiolone, 0.005% ai chlorophacinone, and 0.005% ai diphacinone. One rat per day was offered to mongooses for periods ranging from 1 to 10 days. Exposure to rats fed either chlorophacinone or diphacinone resulted in deaths of 7 of 8 mongooses exposed for 3 to 10 days. Three of four mongooses fed rats that were previously fed bromadiolone were killed, however only 1 mongoose death (of 4 tested) was attributed to brodifacoum. It is noteworthy that although baits registered for rat and mouse control are 50 ppm bromadiolone, the bait used to feed the rats in this study was only 20 ppm.

Evans and Ward (1967) demonstrated that feeding on nutria for several days or more can pose a hazard to minks and dogs when these nutria have been previously been fed diphacinone and warfarin. In this study the rodenticide exposed nutria, with skin, head, tail, feet, and intestines removed, were fed to 3 commercial mink and 3 mongrel dogs. All mink and dogs died within 5 to 17 days of the secondary exposure to diphacinone. The 3 mink exposed to warfarin died within 8 to 15 days. Two of the 3 dogs survived exposure to warfarin for 16 days, although both had bloody feces and one became lethargic.

Others (non-anticoagulants): Fewer secondary-hazard testing has been done with the non-anticoagulant rodenticides, but the available data indicate considerably less hazards than for the anticoagulants. Only 3 (4%) of 77 test animals (foxes, dogs, ferrets, weasels, domestic cats, mink, mongooses) died after feeding on rodents poisoned with zinc phosphide in 10 studies (Table 25). Some regurgitation of prey was reported in animals that died and in some survivors that consumed GI tracts of zinc phosphide-poisoned rodents (Evans 1965, Schitoskey 1975, Hill and Carpenter 1982, Tkadlec and Rychnovsky 1990). Some animals learned to avoid eating the GI tract. In 2 cholecalciferol studies, 18 dogs and 12 feral house cats consumed either poisoned ground rats or brushtail possums (*Trichosurus vulpecula*) for up to 5 days with no deaths, although some reversible signs of toxicosis were reported in the dogs (Table 26). In one study with bromethalin, 4 dogs survived with no observed adverse effects after feeding for 14 days on rats that were poisoned for 1 day (Table 27).

Table 25. Secondary Hazards of Zinc Phosphide to Mammals in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of zinc phosphide toxicity	Reference
Red fox and Gray fox	voles fed bait (86.94 mg ai/kg)	ad lib.	3	4	0	2[a]	Bell and Dimmick 1975
Kit fox	kangaroo rats dosed at 480 mg/rat	1	1	1	0	1[b]	Schitoskey 1975
		1	3	2	0	2[b]	
Dog (domestic)	poisoned nutria carcasses or organs	varied or not reported	varied from 1 to 150 days	8	1	2[b]	Evans 1965
Least weasel	voles fed 5% bait[c]	1	3	2	0	0	Tkadlec and Rychnovsky 1990
Cat (domestic)	voles fed 5% bait[c]	7-11	1-2	2	1	1[b]	
Cat (domestic)	poisoned nutria carcasses or liver	ad lib.	1-10	3	1	2[b]	Evans 1965
Mink	prairie dogs fed 2% ai bait	200 g	30	5	0	0	Tietjen 1976
Mink	poisoned nutria	ad lib.	10	3	0	0	Evans 1965
			20	2	0	0	
Mongoose	rats fed bait (% ai not reported)	10 total	5-10	4	0	0	Pank 1972
Mongoose	rats fed 1% ai bait[c]	5-7 total	35	2	0	0	Doty 1945[d]
Siberian ferret	rats fed 2% bait or orally dosed at 40, 80, or 160 mg/rat	1 rat every other day	10	16	0	13[e]	Hill and Carpenter 1982
European ferret	organs or carcass from prairie dogs fed 2% bait	ad lib.	3	20	0	0	Matschke and Andrews 1990

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of zinc phosphide toxicity	Reference
European ferret	mice	3-4	1	3	0	0	Ueckermann 1982[f]

[a] feeding-behavior irregularities were reported

[b] some prey regurgitated if stomach contents consumed; no other ill effects were observed

[c] baits registered in the U. S. are 2% ai

[d] cited in Johnson and Fagerstone 1994 and Evans 1965

[e] some altered blood chemistry (hemoglobin, globulin, cholesterol, triglycerides) and prey regurgitation was reported

[f] personal communication to G. Joermann (Joermann 1998)

Table 26. Secondary Hazards of Cholecalciferol to Mammals in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of cholecalciferol toxicity	Reference
Cat (domestic)	brushtail possums dosed with 20 mg ai/kg	ad lib.	5	12	0	0	Eason et al. 1996
Dog (domestic)	brushtail possums poisoned with an LD95 dose in cereal bait	1	1	4	0	0	Eason et al. 2000
			2	2	0	0	
			5	12	0	12[a]	

[a] partial anorexia and varying degrees of lethargy from day 4 to 14 after dosing; all recovered

Table 27. Secondary Hazards of Bromethalin to Mammals in Laboratory Studies

Predator/scavenger (p/s)	Prey offered to p/s	No. prey offered daily per p/s	No. days p/s exposed	No. p/s exposed	No. p/s dead	No. survivors with signs of bromethalin toxicity	Reference
Dog (domestic)	ground meat from rats fed 0.005% ai bait for 1 day	600 g	14	4	0	0	van Lier 1981

Potential Primary Risks

Birds

The amount of bait and number of rat-bait pellets (0.2 g each) that birds of various sizes need to eat in a single feeding to obtain a dose expected to be lethal to 50% of the individuals in the population (i.e., LD50 dose) are estimated from the acute oral toxicity for the northern bobwhite or mallard. Estimates of food-ingestion rates (g dry matter per day) are determined from allometric equations in Nagy (1987; cited in EPA 1993): 6.1 g for a 25-g passerine, 9.6 g for a 100-g non-passerine, and 53.9 g for a 1000-g non-passerine. A 25-g passerine can potentially ingest an LD50 dose by consuming 0.02 g zinc phosphide bait (<1 pellet), 0.13 g brodifacoum bait (<1 pellet), 0.26 g difethialone bait (<2 pellets), or 1.2 g (6 pellets) of bromethalin bait (Table 28). Larger non-passerines need to consume more pellets to obtain an LD50 dose but could potentially do so. In contrast, 25- to 1000-g birds would need to eat 100 or more pellets to ingest an LD50 dose of bromadiolone, chlorophacinone, diphacinone, warfarin, or cholecalciferol.

Most of the rodenticide baits, but especially brodifacoum, difethialone, and zinc phosphide, exceed the Agency's LOC for avian dietary risk (Table 29). The Agency presumes potential acute risk when the dietary RQ equals or exceeds 0.5 for non-endangered species and 0.1 for endangered species. Brodifacoum, difethialone, and zinc phosphide exceed the LOC for non-endangered species by 86- to 126-fold for the northern bobwhite and 14- to 50-fold for the mallard. The exceedances are even higher for endangered species.

Table 28. Comparative Risk to Birds From a Single Feeding of Rodenticide, Based on the Amount of Bait Needed to Ingest an LD50 Dose (i.e., a dose lethal to 50% of the individuals in a population)

			25-g passerine			100-g non-passerine			1000-g non-passerine		
Rodenticide	mg ai/kg in bait	LD50[a] (mg ai/kg)	bait (g)	% of daily food intake[b]	no. bait pellets[c]	bait (g)	% of daily food intake	no. bait pellets	bait (g)	% of daily food intake	no. bait pellets
Second-generation anticoagulants											
Brodifacoum	50	0.26	0.13	2.1	0.6	0.52	5.4	2.6	5.2	9.6	26
Difethialone	25	0.26	0.26	4.3	1.3	1.04	10.8	5.2	10.4	19.3	52
Bromadiolone	50	138	69	>100	345	276	>100	1380	2760	>100	>1000
First-generation anticoagulants											
Chlorophacinone	50	258	129	>100	645	516	>100	2580	5160	>100	>1000
Chlorophacinone	100	258	64.5	>100	322	258	>100	1290	2580	>100	>1000
Diphacinone	50	>400	200	>100	1000	800	>100	4000	8000	>100	>1000
Diphacinone	100	>400	100	>100	500	400	>100	2000	4000	>100	>1000
Warfarin	250	620	62	>100	310	248	>100	1240	2480	>100	>1000
Others (non-anticoagulants)											
Bromethalin	100	4.6	1.2	18.8	6	4.6	47.9	23	46	85.3	230
Zinc phosphide	20,000	12.9	0.02	0.3	<0.1	0.07	0.7	0.3	0.7	1.2	3.2
Cholecalciferol	750	>600	20	>100	100	80	>100	400	800	>100	4000

[a] the LD50 values used in the calculations are from northern bobwhite or mallard acute-oral toxicity studies required by the Agency to support pesticide registration (see Tables 3, 4, and 5); ">" values are assumed to be "=" values for the calculations

[b] food ingestion rates (g dry matter per day) are based on the allometric equations of Nagy 1987 (cited in EPA 1993): 6.1 g for a 25-g passerine, 9.6 g for a 100-g non-passerine, and 53.9 g for a 1000-g non-passerine

[c] assuming a bait pellet weighs 0.2 g (information provided by Syngenta Crop Protection, Inc., Greensboro, NC)

Table 29. Avian Dietary Risk Quotients. RQs ≥0.5 (for non-endangered species) or ≥ 0.1 (for endangered species) Exceed the Agency's Level of Concern for Acute Risk to Birds.

Rodenticide	mg ai/kg in bait	Test species	LC50[a] (ppm)	Dietary RQ[b]
Second-generation anticoagulants				
Brodifacoum	50	northern bobwhite	0.8	63
		mallard	2.0	25
Difethialone	25	northern bobwhite	0.5	50
		mallard	1.4	18
Bromadiolone	50	northern bobwhite	37.6	1.4
		mallard	158	0.3
First-generation anticoagulants				
Chlorophacinone	50	northern bobwhite	56	0.9
		mallard	172	0.3
Chlorophacinone	100	northern bobwhite	56	1.8
		mallard	172	0.6
Diphacinone	50	northern bobwhite	>5000	n/a
		mallard	906	<0.1
Diphacinone	100	northern bobwhite	>5000	n/a
		mallard	906	0.1
Warfarin	250	northern bobwhite	625	0.4
		mallard	890	0.3
Others (non-anticoagulants)				
Bromethalin	100	northern bobwhite	210	0.5
		mallard	620	0.2
Zinc phosphide	20,000	northern bobwhite	469	43
		mallard	2885	7
Cholecalciferol	750	northern bobwhite	528	1.4
		mallard	1190	0.6

[a] LC50 values used to calculate the dietary RQs are from dietary toxicity studies required by the Agency to support pesticide registration (see Tables 3, 4, and 5)

[b] RQ = ppm ai in bait/LC50; RQs are not calculated when the LC_{50} value categorizes the active ingredient as practically nontoxic (i.e., LC50 >5000 ppm) to the test species

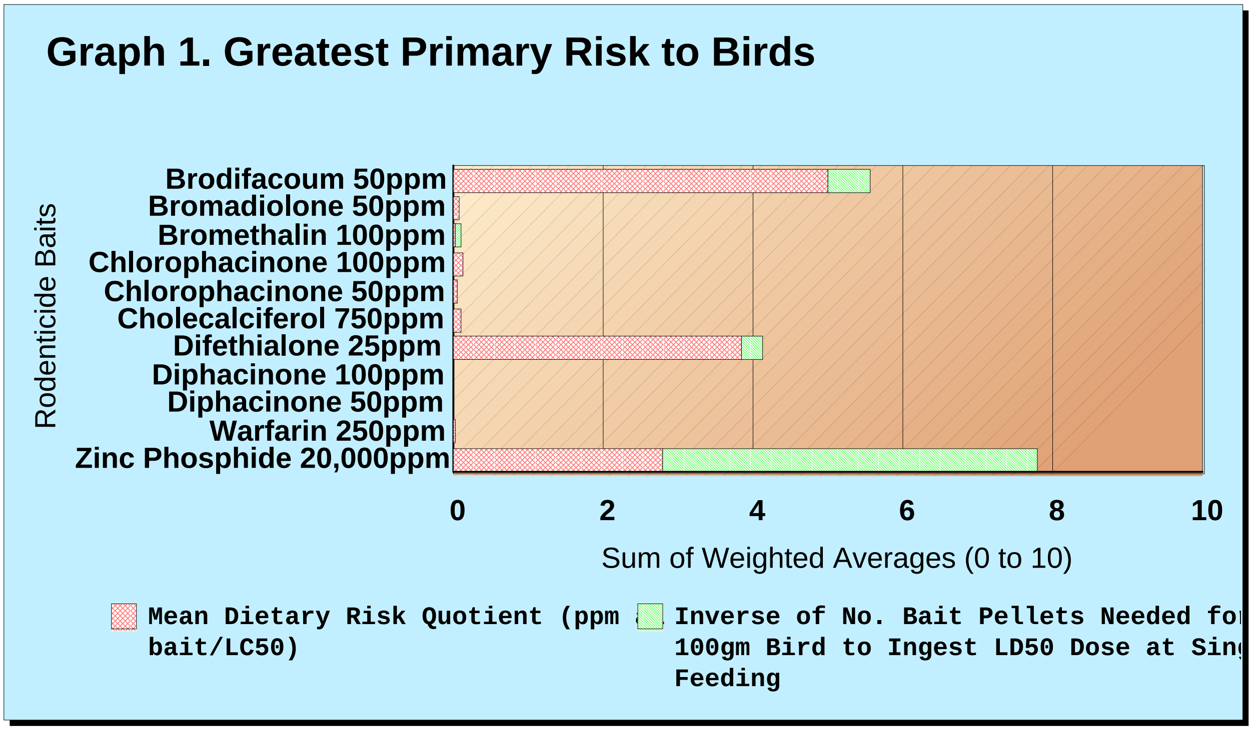
Based on the comparative analysis model, zinc phosphide, brodifacoum, and difethialone stand out as the rodenticides posing the greatest potential primary risk to birds. This result is based on two measures of effect: mean dietary RQ (ppm bait/LC50) and the number of bait pellets needed for a 100-g bird to ingest an LD50 dose in a single feeding. In order to correctly calculate the weighted averages, the inverse of the number of bait pellets needed for a 100-g bird to ingest an LD50 dose in a single feeding was calculated and used in the comparative analysis model. The sum of the weighted average values for all the rodenticides is tabulated in the 'Summary values' column in Table 30 and also is depicted in Figure 2. Brodifacoum has higher summary risk values than difethialone for both measures of effect. The mean dietary RQ appears to be the most significant measure of effect leading to the conclusion that brodifacoum poses greater potential risk to birds than either difethialone or zinc phosphide and that difethialone poses greater potential risk to birds than does zinc phosphide.

Table 30. Comparative Analysis Model Results for Primary Risk to Birds

Rodenticide	mg ai/kg bait	Measure-of-effect values		Summary values
		Mean dietary RQ[a]	Inverse of the LD50 dose for a 100-g bird (no. bait pellets)[b]	
Brodifacoum	50	44.00	0.38	5.58
Bromadiolone	50	0.85	0.00	0.10
Bromethalin	100	0.35	0.04	0.10
Chlorophacinone	100	1.20	0.00	0.14
Chlorophacinone	50	0.60	0.00	0.07
Cholecalciferol	750	1.00	0.00	0.12
Difethialone	25	34.00	0.19	4.15
Diphacinone	100	0.10	0.00	0.01
Diphacinone	50	0.10	0.00	0.01
Warfarin	250	0.35	0.00	0.04
Zinc Phosphide	20,000	24.75	3.33	7.81

[a] from Table 29
[b] from Table 28

Figure 2. Comparative Analysis Model Summary Values For Primary Risk to Birds



Primary risk to birds also is analyzed by an alternative approach, using an HD_5(50%) reference value to calculate the amount of bait needed to provide an LD50 dose to a 100-g bird instead of the LD50 values for bobwhite quail or mallard ducks. The HD_5(50%) is the 5% tail of the avian LD50 toxicity distribution calculated with 50% probability of overestimation (Mineau et al.2001). The authors believe that the *"approach of using reference values based on species specific extrapolation factors represents the most unbiased attempt to date to compare the toxicity of pesticides for which many data points are available with those about which we know very little."* Utilizing the HD_5(50%) reference value, rather than the LD50, does not change the rankings (see Attachment C for more details, including reference values for the rodenticides and a graphical comparison of the summary measures of effect for each of the 2 approaches).

Findings from experimental studies conducted in field or other outdoor settings, along with information obtained during operational programs, provide useful data linking exposure to adverse effects in birds. Zinc phosphide, chlorophacinone, and diphacinone are registered for field and other outdoor uses, and brodifacoum has been used to control introduced rats on some U. S. oceanic islands. Such uses often allow broadcast or other unprotected applications (e.g., spot-baiting) that exposes bait to birds that might be attracted to grain pellets or treated grains (e.g., corn, wheat, oats).

Howald et al. (1999) reported nontarget effects to birds during a brodifacoum rat-control program on Langara Island, Canada. Thirteen common ravens (*Corvus corax*) were found dead 12 to 47 days after baiting began, and all had brodifacoum residue (0.985 to 2.522 ppm) in their liver. Remains of 7 other ravens also were found but not analyzed. At least 8 bait stations were raided by ravens, which either reached into the stations and pulled out bait blocks or tipped the stations to roll out the bait, even though the stations were secured. Some of the ravens also fed on poisoned rats. Brodifacoum also was detected in a pooled sample of 3 northwestern crows (*C. caurinus*) collected 12 days after the start of baiting.

Brodifacoum also was detected in song sparrows (*Melospiza melodia*) collected by shotgun on Langara Island (Howald 1997). Residue levels of 0.643 and 0.567 ppm were detected in 2 of 4 pooled liver samples (2 to 3 individuals per sample) and 0.058 ppm in 1 pooled sample (4 individuals) analyzed for whole-body residue. It is not known how the sparrows were exposed or whether any died. They may have consumed bait crumbs found scattered around bait stations and along rat runways but also might have eaten invertebrates that fed on bait. Howald (1997) also found that snails (*Vespericola* sp., *Haplotrema* sp.) and banana slugs (*Ariolimax* sp.) commonly fed on brodifacoum bait and may pose a risk to birds and nontarget mammals that consume them.

Godfrey (1985) cited an incident at an aviary where several birds (avocets, pittas, plovers, finches, thrushes, warblers, crakes, honey creepers) died after being exposed to brodifacoum. Brodifacoum concentrations of 0.081 to 1.69 ppm were reported in tissues of dead birds. Because bait was applied in bait stations, it was assumed that the birds were exposed by feeding on pavement ants and cockroaches that had eaten bait.

Brodifacoum baits (20 ppm or 50 ppm) are used for field control of rats and brushtail possums in New Zealand, and much useful information on nontarget risks has been reported. However, because of increased concerns about nontarget mortality and movement of brodifacoum through the food chain, its use is being reviewed and curtailed in many areas in New Zealand (Eason and Murphy 2001). The following studies provide further information on primary risks to birds, based on mortality reported during field studies or operational control programs.

Eason and Spurr (1995) reviewed the impacts of brodifacoum baiting on nontarget birds during baiting programs in New Zealand, where bait is applied in bait stations (50 ppm cereal-based wax blocks) or aerially broadcast (20 ppm pellets) in a single application. They report mortality of a wide range of bird species, including 33 indigenous species or subspecies and 8 introduced species or subspecies, and presume most resulted from primary exposure. Populations of indigenous rails (weka, *Gallirallus australus*; pukeko, *Porphyrio porphyrio*) monitored during rodenticide baiting operations were severely reduced: "For example, the entire population of western weka on Tawhitinui island were exterminated by consumption of Talon® 50WB intended for ship rats, which they obtained by reaching into bait stations, by eating baits dropped by rats, and by eating dead or dying rats (Taylor 1984)." On another island, 80 to 90% of the Stewart Island weka population was killed by baits applied for Norway rats. Aerial application of 0.002% bait on two other islands reduced a weka population by about 98% and a pukeka population by >90%. Numbers of quail, blackbirds, sparrows, and myna were markedly reduced on another island. Some other species suffered no apparent adverse effects.

Dowding et al. (1999) found numerous dead birds after an aerial baiting operation to eradicate rats and mice and reduce rabbit numbers on Motuihe Island, New Zealand. Brodifacoum bait (20 ppm) was applied twice, with 9 days between applications. Nontarget species were monitored, including pukeka (3 groups of 98 birds), a flock of 52 paradise shelduck (*Tadorna variegata*), 8 New Zealand dotterels (*Charadrius obscurus*), and 14 variable oystercatchers (*Haematopus unicolor*). There was no evidence that dotterels or oystercatchers were adversely affected, but mortality of pukeko and shelduck was 49% and 60%, respectively. Birds of 10 species were found dead. The liver from each of 29 dead birds of 10 species was analyzed. All livers contained brodifacoum residue, with mean levels per species ranging from 0.56 to 1.43 ppm. Chaffinch (*Fringilla coelebs*), North Island robin (*Persica australis longipes*), North Island weka, and North Island saddleback (*Philesturnus carunculatus rufusater*) also were found dead after a brodifacoum baiting on Mokoia Island, New Zealand (Stephenson et al.1999).

Eason and Spurr (1995) report that invertebrates have been observed eating brodifacoum bait, and residues were detected in beetles collected in bait stations in New Zealand. Invertebrates have different blood-clotting mechanisms than vertebrates and may not be affected by anticoagulants, but insectivorous animals feeding on the contaminated invertebrates might be at risk. Robertson et al. (1999) monitored brown kiwis (*Apteryx mantelli*) potentially at risk from brodifacoum applications in bait stations placed for possum control. Although there was no evidence that adult kiwi died as a result of the applications, including 55 that were radio-tagged, brodifacoum was detected at levels of 0.01 to 0.18 ppm in 3 of 4 chicks found dead from unknown causes. The authors speculated that the chicks may have obtained bait or may have eaten invertebrates that ingested bait. The death of an endangered Seychelles magpie-robin (*Copsychus sechellarum*) on Fregate Island, Seychelles, was likely due to its feeding on insects that had taken brodifacoum baits from bait stations (Thorsen et al. 2000). Loss of bait, attributed mostly to consumption by millipedes, crabs, and skinks, averaged 17% per night.

Hegdal (1985) conducted a study in Washington to examine risks to game birds from a 0.005% ai diphacinone bait applied for vole control in orchards. Most orchards were treated twice, with 20 to 30 days between treatments, at an average rate of 12.9 kg/ha (11.5 lb/acre). Telemetry was used to monitor the fate of 52 ring-necked pheasants, 18 California quail, and 30 chukar potentially exposed to the bait. About half of the quail and all chukar were pen-raised and had been released into the orchards. Dead game birds and other animals found were necropsied and any available tissue collected for residue analysis. Eight of 30 pheasants, 9 of 15 quail, and 1 of 10 chukar collected by the researchers or shot by hunters contained diphacinone residue in the liver. Bait made up as much as 90% of crop contents of some birds. No residue was detected in 4 passerines collected 31 to 73 days after treatment. The author concluded that risk to game birds in orchards appeared to be low but emphasized that substantial quantities of bait were eaten and longer-term behavioral and physiological effects, such as susceptibility to predation, need to be considered along with direct mortality in order to evaluate potential hazards from exposure.

Some information on potential nontarget risks was gained during field studies conducted to assess the efficacy of 0.01% ai and 0.005% ai diphacinone and chlorophacinone baits against California ground squirrels inhabiting rangeland (Baroch 1994 a,b; 1996a,b). For each of these rodenticides, trials included separate spot-baiting applications with 0.01% ai and 0.005% ai grain baits and a trial in which 0.005% ai grain bait was only available in bait stations. Searches for nontarget carcasses were made on and around treated plots after baiting. One dead dove and 2 dead roadrunners (*Geococcyx californicus*) were found on treatment plots, but there was no evidence that these birds had eaten any bait.

Hegdal and Gatz (1977) evaluated risks to nontarget wildlife from zinc phosphide bait (2% ai) broadcast by ground or air at rates of 5 to 10 lb per acre for vole control in Michigan orchards. Carcass searches were made across 672 of 950 treated acres in the 2 weeks after treatment. Bird carcasses recovered included 1 blue jay (*Cyanocitta cristata*) and 1 of 5 radio-equipped pheasants. Northern bobwhite were observed, and some were seen feeding on bait, but no carcasses were found.

Ramey et al. (1998) examined risk to radio-collared ring-necked pheasants from zinc phosphide baiting in alfalfa fields in California. Pheasants were rarely found in fields when bait was applied after the alfalfa was cut. The pheasants preferred other habitats at this time, and none died as a result of the baiting. Results were somewhat confounded by the use of some pen-reared pheasants, most of which were quickly taken by predators.

Johnson and Fagerstone (1994) reviewed a number of field studies conducted to evaluate primary effects of zinc phosphide on nontarget wildlife for the following uses: prairie dogs, ground squirrels, and jackrabbits on rangeland; California ground squirrels and rats on ditch banks; voles and rats in orchards; and rats in sugarcane. They also note that some information on nontarget hazards has also been gathered for use against voles in alfalfa and muskrats and nutria in wetlands. They concluded: "Although field studies to determine effects of zinc phosphide on nontarget wildlife have generally found no significant effects, under certain circumstances operational zinc phosphide applications have resulted in mortality of nontarget wildlife."

Quy et al. (1995) observed small song birds, especially chaffinches, that had difficulty flying and appeared to be ill during a rat-control operation with calciferol bait in the United Kingdom. A number of dead birds were found; all had abnormally high calcium deposits in their kidneys, suggesting calciferol toxicosis.

Nontarget mammals

The amount of bait and number of rat-bait pellets that nontarget mammals of various sizes need to eat in a single feeding to obtain an LD50 dose (i.e., the dose expected to be lethal to 50% of the individuals in the population) is estimated from the acute oral toxicity for the laboratory rat. Estimates of food-ingestion rates (g dry matter per day) are determined from allometric equations in Nagy (1987; cited in EPA 1993): 3.8 g for a 25-g rodent, 8.3 g for a 100-g rodent, and 68.7 g for a 1000-g mammal. A 25-g rodent can potentially ingest an LD50 dose by consuming less than 1 g (~5 pellets) of most baits, and a single pellet of zinc phosphide or brodifacoum can provide this dose (Table 31). Larger mammals also are potentially at risk if they eat baits of most of these rodenticides. For warfarin, there is some uncertainty that a single feeding would be lethal to most individuals, because warfarin is reported to require multiple feedings over a period of a few days to be efficacious (Papworth 1958, Jackson and Ashton 1992, Timm 1994).

Dietary RQs are calculated for brodifacoum, bromadiolone, and the 3 first-generation anticoagulants (Table 32). RQs cannot be determined for difethialone and the 3 non-anticoagulants, because dietary data are not available. The RQs exceed the LOC 48- to 188-fold for non-endangered mammals and 240- to 943-fold for endangered mammals. This indicates a significant risk to nontarget mammals that feed on any of these baits.

Based on the comparative analysis model, zinc phosphide is ranked as the rodenticide posing the greatest potential primary risk to nontarget mammals, with brodifacoum ranked a distant second, and warfarin and bromadiolone an even more distant third and fourth. The results are based on a single measure of effect: the number of bait pellets needed for a 100-g mammal to ingest an LD50 dose in a single feeding. In order to correctly calculate the weighted averages, the inverse of the number of bait pellets needed for a 100-g mammal to ingest an LD50 dose in a single feeding was calculated and used in the comparative analysis model. The sum of the weighted average values for all the rodenticides is tabulated in the ‘Summary values' column in Table 33 and presented graphically in Figure 3.

Table 31. Comparative Risk to Mammals From a Single Feeding of Rodenticide, Based on the Amount of Bait Needed to Ingest an LD50 Dose (i.e., a dose lethal to 50% of the individuals in a population)

			25-g rodent			100-g rodent			1000-g mammal		
Rodenticide	mg ai/kg in bait	LD50[a] (mg ai/kg)	bait (g)	% of daily food intake[b]	no. bait pellets[c]	bait (g)	% of daily food intake	no. bait pellets	bait (g)	% of daily food intake	no. bait pellets
Second-generation anticoagulants											
Brodifacoum	50	0.4	0.2	5.2	1	0.8	9.6	4	8	11.6	40
Difethialone	25	0.55	0.56	14.7	2.8	2.2	26.5	11	22	32	110
Bromadiolone	50	0.7	0.35	9.2	1.8	1.4	16.2	7	14	20.4	70
First-generation anticoagulants											
Chlorophacinone	50	6.2	3.1	81.6	15.5	12.4	>100	62	124	>100	620
Chlorophacinone	100	6.2	1.6	42	8	6.2	74.7	31	62	90.2	310
Diphacinone	50	2.3	1.2	31.6	6	4.6	55.4	23	46	67	230
Diphacinone	100	2.3	0.6	15.8	3	2.3	27.7	11.5	23	33.5	115
Warfarin	250	3	0.3	7.9	1.5	1.2	14.5	6	12	17.5	60
Others (non-anticoagulants)											
Bromethalin	100	9.9	2.5	65.8	12.5	9.9	119	49.5	99	>100	495
Zinc phosphide	20,000	21	0.03	0.7	0.13	0.1	1.2	0.5	1	1.5	5
Cholecalciferol	750	42	1.4	36.8	7	5.6	67.5	28	56	81.5	280

[a] the LD50 values used in the calculations are from laboratory rat or mouse acute-oral toxicity studies required by the Agency to support pesticide registration (see Tables 6, 7, and 8); the tabulated value is provided as an average if the LD50 differed between male and female

[b] food ingestion rates (g dry matter per day) are based on the allometric equations of Nagy 1987 (cited in EPA 1993): 3.8 g for a 25-g rodent, 8.3 g for a 100-g rodent, and 68.7 g for a 1000-g mammal

[c] assuming a bait pellet weighs 0.2 g (information provided by Syngenta Crop Protection, Inc., Greensboro, NC)

Table 32. Mammalian Dietary Risk Quotients. RQs ≥0.1 (endangered species) or ≥0.5 (non-endangered species) Exceed the Agency's Level of Concern for Acute Risk to Mammals.

Rodenticide	mg ai/kg in bait	Test species	LC50[a] (ppm)	Dietary RQ[b]
Second-generation anticoagulants				
Brodifacoum	50	laboratory rat	0.53	94.3
Bromadiolone	50	laboratory rat	0.92	54.3
First-generation anticoagulants				
Chlorophacinone	50	laboratory rat	1.14	43.8
Chlorophacinone	100	laboratory rat	1.14	87.7
Diphacinone	50	laboratory rat	2.08	24.0
Diphacinone	100	laboratory rat	2.08	48.1
Warfarin	250	laboratory rat	4.41	56.7

[a] LC50 values used to calculate the dietary RQs are from dietary toxicity studies conducted by the Agency's former Toxicology Section (see Tables 6 and 7); mammalian dietary data are not available for difethialone, bromethalin, zinc phosphide, and cholecalciferol

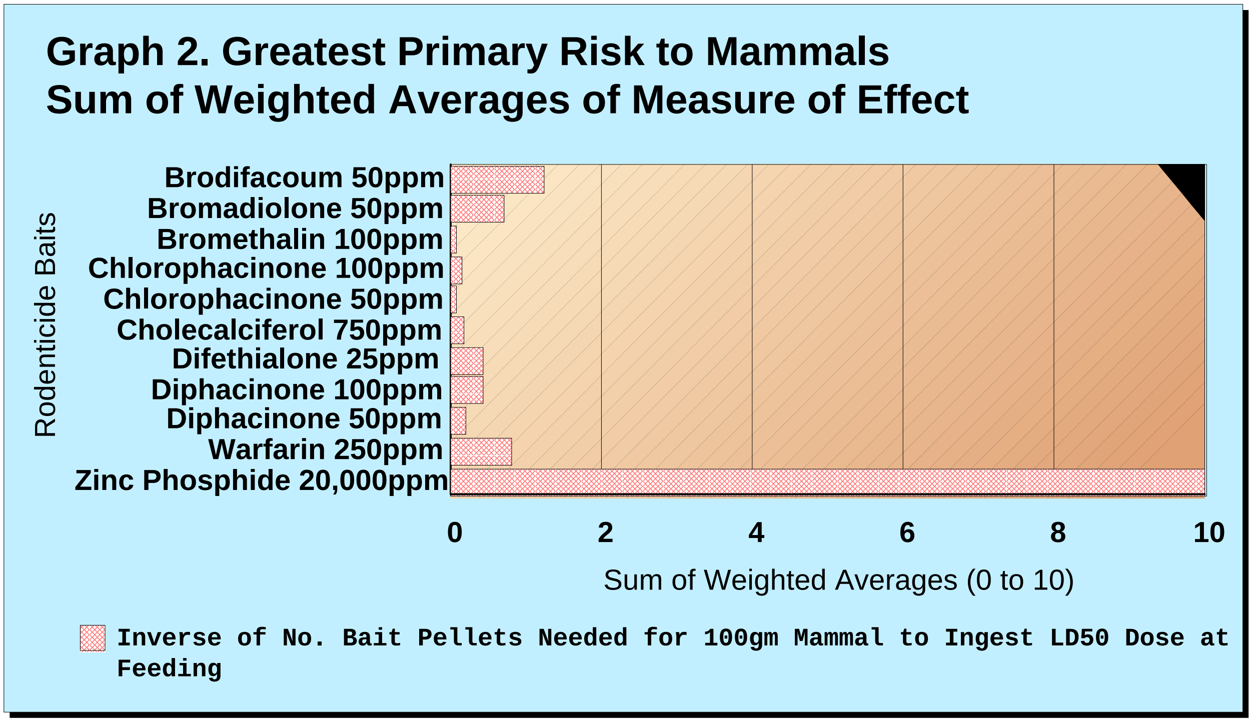
[b] RQ = ppm ai in bait/LC50

Table 33. Comparative Analysis Model Results for Primary Risk to Nontarget Mammals

Rodenticide	mg ai/kg bait	Inverse of the LD50 dose for a 100-g rodent (no. bait pellets)[a]	Summary value
Brodifacoum	50	0.25	1.25
Bromadiolone	50	0.14	0.71
Bromethalin	100	0.02	0.10
Chlorophacinone	100	0.03	0.16
Chlorophacinone	50	0.02	0.08
Cholecalciferol	750	0.04	0.18
Difethialone	25	0.09	0.45
Diphacinone	100	0.09	0.43
Diphacinone	50	0.04	0.22
Warfarin	250	0.17	0.83
Zinc Phosphide	20,000	2.00	10.00

[a] from Table 31

Figure 3. Comparative Analysis Model Summary Values For Primary Risk to Nontarget Mammals



The little information available on primary risk to mammals in the field has mostly come from animals found dead or moribund on treatment plots during efficacy trials and from an operational control program on a Canadian island. Howald (1997) reported that dusky shrews (*Sorex monticolus*) entered bait stations and fed on brodifacoum bait during a rat-control program on a Canadian island. By day 20 of baiting, shrews had eaten bait in 80% of the 42 rat bait stations. The shrew population declined sharply but rebounded to about half the prebaiting level after baiting stopped in 1994; however, shrew numbers declined further when baiting resumed in 1995. The long-term impact of baiting on the shrew population is unclear. No difference in population size was found pre- and post-baiting on a larger, adjacent island.

Some information on nontarget risks was gained during studies conducted to assess the efficacy of 0.01% ai and 0.005% ai chlorophacinone and diphacinone baits against California ground squirrels inhabiting rangeland. Baroch (1996a,b) applied chlorophacinone bait by spot-baiting or in bait stations, and treatment plots were searched periodically for target and nontarget carcasses . Thirty-six nontarget deer mice, San Joaquin pocket mice (*Perognathus inornatus*), and woodrats were found dead; based on the presence of blue dye incorporated into the bait and/or signs of internal or external hemorrhaging, mortality of 31 (86%) mice was attributed to the baiting. Four dead desert cottontails (*Sylvilagus auduboni*) and 2 dead Botta's pocket gophers (*Thomomys* *bottae*) also were collected, but there was no evidence that these had been exposed to bait. In another study designed to assess the efficacy of chlorophacinone and diphacinone baits, some small mammals, especially kangaroo rats (*Dipodomys* spp.), were found dead on treated plots (Salmon et al. 2002). Collectively, these studies indicate that some small nontarget mammals will be killed when these baits are applied for controlling ground squirrels.

Comparative Toxicokinetics: Absorption, Metabolism and Excretion of Anticoagulants

Considerable differences exist in absorption, metabolism and excretion of the anticoagulants, which may have important consequences for both primary and secondary risk. A compound that is rapidly metabolized or excreted from a primary consumer may result in a lesser risk than one that bioaccumulates with repeated sublethal exposure, even if repeated exposure occurs weeks or even months after initial exposure (Eason and Murphy 2000). Those compounds more rapidly cleared from the body are less likely to pose such long-term risk. The available information indicates that the second-generation anticoagulants are much more persistent in animal tissue than are the first-generation anticoagulants. Data also suggest that brodifacoum may be more persistent than either difethialone or bromadiolone. Few data exist for the non-anticoagulants but, based on lack of toxicity in secondary tests, apparently they are not retained in toxicologically significant amounts in animal tissues.

Most of the available information is from studies that examined elimination and retention following a single, sublethal oral dose of anticoagulant. In a baiting situation, however, rats or mice will not die for several days or more after ingesting a lethal dose and may continue consuming bait. A wild Norway rat may ingest as many as 80 brodifacoum LD50 doses if feeding only on bait and as many as 40 LD50 doses if offered a choice of bait or untreated food (ICI Americas, Inc. 1978b). In a situation of repeat exposure for several days or more, anticoagulant may circulate in the blood at higher levels and for a longer time than suggested by studies in which only a single, sublethal dose was administered (Belleville 1981).

Elimination of anticoagulants from the body is sometimes described as rapid (e.g., Poché 1986, Kaukeinen et al. 2000). However, such characterizations usually refer to the rapid excretion of unbound or unabsorbed material being excreted principally in feces during the first few days after administration. Alternatively, it may refer to the clearance from the blood as compared with tissue retention. Rather than concentrating on the amount of anticoagulant excreted, risk assessments should focus on the material retained in the body after single and multiple exposures. The studies summarized below indicate the differences among these compounds and their potential to bioaccumulate with repeat exposure.

Second-generation anticoagulants

Second-generation compounds are not readily metabolized, and the major route of excretion of unbound compound is through the feces. After absorption, high concentrations circulate in the blood and are rapidly established in the liver and other tissues. Half-lives in the blood of rats are 1.0 to 1.4 days for bromadiolone and 6.5 days for brodifacoum (Table 34). Elimination from liver is much slower and biphasic, with a very prolonged terminal phase. It is apparent from the studies discussed below that a proportion of any ingested dose of a second-generation anticoagulant bound in the liver, kidney, or pancreas remains in a stable form for some time and is only very slowly excreted.

Hawkins et al. (1991) administered brodifacoum and bromadiolone to rats in a single oral dose of 0.2 mg ai/kg. Elimination was biphasic, with half-lives of 63 days for brodifacoum and 17 days for bromadiolone in the initial 28 days and 282 and 318 days, respectively, in the terminal phase. These differences are not statistically significant, but mean liver concentrations of brodifacoum were significantly higher for brodifacoum throughout the study (Table 35).

Bratt and Hudson (1979) found that radiolabeled brodifacoum was rapidly and almost completely absorbed when administered to rats in a single oral dose (0.25 mg ai/kg). After 10 days, about 11 to 14% had been eliminated in urine and feces, but 74.6% of the dose was still retained in body tissues. Almost half the dose administered was detected in the carcass and skin, with lesser amounts in the liver (22.8%), pancreas (2.3%), kidney (0.8%), spleen (0.2%), and heart (0.1%). The estimated half-life of brodifacoum in rat tissues was estimated to be 150 to 200 days.

Batten and Bratt (1987) orally dosed male rats with a single dose of radiolabeled brodifacoum at doses of either 0.02. 0.15, or 0.35 mg ai/kg. The highest concentration of radioactivity in the liver was found 1 day after dosing, but 21 to 34% of the dose was still detected after 13 weeks and >11% after 104 weeks (Table 36). The elimination half-life for the 2 lowest doses was 350 days. For rats dosed at 0.35 mg ai/kg, a near-lethal dose (LD50 = 0.39 to 0.56 mg ai/kg), elimination from the liver was biphasic and consisted of a rapid phase (days 1 to 4) in which the half-life was approximately 4 days and a slower phase (days 28 to 84) in which the half-life was 128 days. Two rats dosed at that level died during the study. Signs of brodifacoum toxicosis were observed in some survivors. Some dosed rats also had gained less body-weight and displayed signs of internal hemorrhage when dissected.

Table 34. Persistence of Second-generation Anticoagulants in Blood and Liver

Anticoagulant	Species	Dose (mg ai/kg)	No. doses	Blood $t_{1/2}$[a] (days)	Liver retention[a,b] (days)	Reference
Brodifacoum	rat	0.02 or 0.15	1		350[c] ($t_{1/2}$)	Batten and Bratt 1990
		0.35	1		128[d] ($t_{1/2}$)	
Brodifacoum	rat	0.2	1		282 ($t_{1/2}$)	Hawkins et al. 1991
Brodifacoum	rat	0.25	1		150-200 ($t_{1/2}$)	Bratt and Hudson 1979
Brodifacoum	rat	0.06	4 (at weekly intervals)		136 ($t_{1/2}$)	Belleville 1991
Brodifacoum	rat	0.35	1		130 ($t_{1/2}$)	Parmar et al. 1987
Brodifacoum	rat			6.5	>80	Bachmann and Sullivan 1983[e]
Brodifacoum	possum	0.1	1	20-30	>252	Eason et al. 1996
Brodifacoum	rabbit			2.5		Breckenridge et al. 1985[e]
Brodifacoum	sheep	0.2 or 2.0	1		>128	Laas et al. 1985
Brodifacoum	dog			6		Woody et al. 1992[e]
Brodifacoum	dog			0.9-4.7		Robben et al. 1998[e]
Brodifacoum	human			0.7-1.5		Weitzel et al. 1990[e]
Difethialone	rat	0.5	1	2.3	126 ($t_{1/2}$) (175%, 98&)	Belleville 1986
Difethialone	rat	0.06	4 (at weekly intervals)		74 ($t_{1/2}$)	Belleville 1991
Difethialone	dog			2.2-3.2		Robben et al. 1998[e]

Anticoagulant	Species	Dose (mg ai/kg)	No. doses	Blood $t_{1/2}$[a] (days)	Liver retention[a,b] (days)	Reference
Bromadiolone	rat	0.2	1		318 ($t_{1/2}$)	Hawkins et al. 1991
Bromadiolone	rat	0.93	1	1.0-1.1	170 ($t_{1/2}$)	Parmar et al. 1987
Bromadiolone	rat	0.8 3.0	1 1	1.1 2.4		Kamil 1987[e]
Bromadiolone	sheep	2.0	1		256	Nelson and Hickling 1994[e]

[a] $t_{1/2}$ for plasma and liver is the elimination half-life ($-phase)

[b] liver retention is expressed as either the time period for which residues persist or as the elimination half-life

[c] the elimination half-life of 350 days is for a single oral dose of 0.02 or 0.15 mg ai/kg; elimination was not biphasic

[d] the elimination half-life of 128 days is the terminal phase for a single oral dose of 0.035 mg ai/kg; elimination was biphasic

[e] cited in Eason et al. (2001)

Table 35. Hepatic Concentrations of Brodifacoum and Bromadiolone in Rats Administered a Single Oral Dose of 0.2 mg ai/kg (adapted from Hawkins et al. 1991)

Days after dosing	Brodifacoum (ppm)	Bromadiolone (ppm)
1	1.107 ± 0.038	0.983 ± 0.049
7	1.078 ± 0.088	0.844 ± 0.051
14	1.121 ± 0.077	0.727 ± 0.098
50	0.838 ± 0.075	0.440 ± 0.042
100	0.679 ± 0.061	0.366 ± 0.026
200	0.539 ± 0.028	0.282 ± 0.041

Table 36. Percentage of a Single Dose of Brodifacoum Retained in the Liver for up to 104 Weeks (adapted from Batten and Bratt 1987)

Time after dosing	% of dose retained per group		
	0.02 mg ai/kg	0.15 mg ai/kg	0.35 mg ai/kg
Day 1	47.3	29.7	28.9
Week 4	39.2	37.1	23.5
Weeks 12-13	34.0	31.7	21.2
Week 65	16.0	15.4	-
Week 104	11.8	11.7	-

Based on those findings, the authors conclude that the existence of biphasic kinetics in the liver for brodifacoum has two important consequences. "Firstly the fast and slow phases can each be characterized by a half-life estimation. It is apparent however that the half-life quoted (approximately 4 days) using data from the fast initial phase of the elimination from the liver can give a misleading impression of the potential persistence of an anticoagulant. If lethal doses were used, tissue concentrations could only be measured prior to death and since this would occur during the rapid elimination phase the subsequent slow phase of elimination would not be apparent. This probably explains why data for bromadiolone, a structurally similar anticoagulant to brodifacoum suggest that this substance is rapidly eliminated from rats (Poché 1986). Secondly, the concentration of radioactivity in the liver at the beginning of the terminal phase is independent of the dose and therefore when expressed as a percentage of the dose decreases as the dose increases. This can give a misleading impression with regard to the size of the residue present."

Parmar et al. (1987) also reported biphasic elimination of radio-labelled brodifacoum and bromadiolone from rat liver. The initial phase occurred from days 2 to 8 after dosing, followed by a prolonged terminal phase when the elimination half-lives were 130 and 170 days for brodifacoum and bromadiolone, respectively. However, the results were presented only in an abstract with too few details provided to adequately evaluate the results reported.

Belleville (1991) orally dosed rats with 0.06 mg ai/kg brodifacoum or difethialone on 4 occasions at weekly intervals. After 6 months, 21% of the total brodifacoum dose and 7% of the total difethialone dose was retained in hepatic tissue (Table 37). Hepatic half-lives calculated for the 158 days after the final dose (days 22 to 180) were 136 days for brodifacoum and 74 days for difethialone.

Table 37. Hepatic Concentrations in Rats Dosed at 0.06 mg ai/kg on Days 0, 7, 14, and 21 (adapted from Belleville 1991)

Time after initial dose	Brodifacoum (ppm)	Difethialone (ppm)
22 days	2.01 ± 0.15	1.28 ± 0.15
49 days	1.50 ± 0.48	0.84 ± 0.15
77 days	0.98 ± 0.32	0.49 ± 0.08
4 months	0.85 ± 0.15	0.35 ± 0.07
6 months	0.87 ± 0.16	0.29 ± 0.08

Studies in species other than rats also indicate that brodifacoum can be retained in animal tissue for a very long time. Eason et al. (1996) detected brodifacoum residue 9 months after administration of a sublethal dose of 0.1 ppm in possums. Laas et al. (1985) examined retention of brodifacoum in sheep tissues and its excretion via feces after a single, sublethal oral dose of either 0.2 or 2.0 mg ai/kg to 14 sheep. Sheep were sacrificed periodically 2 to 128 days after dosing and liver, carcass, and fat tissues analyzed for residue. Brodifacoum was detected in the liver after 128 days, at concentrations of 0.64 and 1.07 mg ai/kg dry weight (equivalent to 0.22 and 0.36 mg ai/kg wet weight), respectively, for the 2 doses. Residue also was detected for up to 8 days in fat and up to 15 days in the carcass. Bromadiolone was detected for 256 days in the liver of sheep that received a sublethal dose of 2 mg ai/kg (Nelson and Hickling 1994). Breckenridge et al. (1985) reported a plasma elimination half-life of about 2.5 days for rabbits dosed with brodifacoum, and Woody et al. (1992) observed an elimination half-life for brodifacoum in serum of 6± 4 days in four dogs. The plasma half-life of brodifacoum determined in three human patients with severe bleeding disorders was found to be approximately 16–36 days (Weitzel et al. 1990).

First-generation anticoagulants

Although fewer data are available for the first-generation anticoagulants (Table 38), the available information indicates they are generally less persistent in the blood and body tissues. Belleville (1981) orally administered radio-labeled chlorophacinone to rats with either a single dose of 1 to 1.26 mg ai/rat (~4 to 6 mg ai/kg) or 3 daily doses of 1.43 mg ai/rat (~6 to 7 mg ai/kg). The compound was rapidly absorbed and metabolized; 90% was excreted within 48 h and 100% within 4 days. Elimination was almost totally via the feces; <1% was via urine and CO_2. The $t_{1/2}$ in blood was 9.8 h, with the maximum concentration attained after 4 to 8 h. The maximum blood concentration in rats that received 3 doses was 1.8 to 3.7 times higher than that from rats receiving a single dose. Concentrations in body tissues after 4 h and 48 hours were highest in liver, but chlorophacinone also was present in kidneys, lungs, heart, muscle, fat, and other parts of the carcass (Table 39).

Yu et al. (1982) studied the metabolism and disposition of diphacinone in rats and mice. In rats given a single oral dose of radiolabeled diphacinone at either 0.18 or 0.4 mg ai/kg, about 70% of the dose was eliminated in feces and 10% in urine within 8 days, whereas about 20% of the dose was retained in body tissues. Mice given a single dose of 0.6 mg ai/kg eliminated most diphacinone within 4 days, and only 7% was retained in body tissues. In both rats and mice, most radioactivity (59 to 69%) was detected in the liver and the kidneys (9 to 12%). Radioactivity also was detected in the brain, heart, spleen, lungs, blood, muscle, fat, and gonads. Several major metabolites were identified, and parent diphacinone in excreta and liver accounted for only about 20% of the dose. In another study, cattle that received a single injection of 1 mg ai/kg had almost constant residue concentrations in liver and kidney at 30, 60, and 90 days after dosing (Bullard et al. 1976). The plasma half-life in humans is reported to be 15 to 20 days (WHO 1995).

Table 38. Persistence of First-generation Anticoagulants in Blood and Liver

Anticoagulant	Species	Dose (mg ai/kg)	No. doses	Blood $t_{1/2}$[a] (days)	Liver retention[a,b] (days)	Reference
Diphacinone	cattle	1.0	1		>90	Bullard et al. 1976
Diphacinone	human			15-20		WHO 1995
Chlorophacinone	rat	4-5	1	0.4		Belleville 1981
Warfarin	rat			0.7 (%) 1.2 (&)		Pyrola 1968[c]
Warfarin	rabbit			0.2		Breckenridge et al. 1985[c]
Warfarin	possum			0.5		Eason et al. 1999
Warfarin	human	0.5-100	1	0.6-2.4		O'Reilly et al. 1963[c]
Warfarin	pig				30-40	O'Brien et al. 1987[c]

[a] $t_{1/2}$ for plasma and liver is the elimination half-life ($-phase)

[b] liver retention is expressed as either the time period for which residues persist or as the elimination half-life

[c] cited in Eason et al. (2001)

Table 39. Chlorophacinone Residue in Rats 4 and 48 hours After an Oral Dose of 1.26 mg ai per Rat (adapted from Belleville 1981)

Tissue	µg ai/g (ppm)	
	4 h after dosing	48 h after dosing
Liver	31.1	2.9
Kidney	6.6	1.2
Lung	4.5	0.4
Heart	3.1	0.2
Muscle (thigh)	2.0	0.1
Fat	1.2	0.7
Carcass	5.2	0.3

Diaz and Whitacre (1976) orally dosed rats with diphacinone (0.32 mg ai/kg/day) for 1 or 2 days. Rats dosed for 2 days were sacrificed 72 h after the second dose and those dosed for 1 day were sacrificed after 48 h. In rats dosed for 2 days, about 45% of the total dose administered was excreted (86% in feces, 14% in urine) and 25% was retained in body tissues 72 h after the last dose. The remaining 30% of the dose was not recovered. The body tissues retaining the most diphacinone at 96 h were the hide and tail, liver, intestine, blood, and the carcass (Table 40). In rats dosed for 1 day and sacrificed after 48 h, about 5% of the dose was excreted and 61% retained; the remained was not recovered.

In contrast to other anticoagulants, especially the second-generation compounds, warfarin is extensively metabolized and the major route of excretion is in the urine. Limited data exist regarding persistence of warfarin in the liver. O'Brien et al. (1987; cited in Eason et al. 2001) found comparatively rapid clearance of warfarin in pigs, with concentrations declining to very low levels after approximately 30 days. Meehan (1984) states that approximately half the warfarin consumed by a rat remains in the body after 6 hours. Thijssen (1995) cites a half-life of 7 to 10 days in animal tissue, and Ford (1993; cited in Poché and Mach 2001) reported a half-life of 42 hours in the gastro-intestinal tract. EPA (1982) noted that only 7.6% of the warfarin consumed in bait by 11 rats remained in the carcass after a 5-day feeding period. According to Machlin (1984; cited in Poché and Mach 2001), warfarin concentrates in the liver, but the adrenal glands, lungs, bone marrow, kidneys, and lymph nodes also contain measurable amounts. Breckenridge et al. (1985) reported a plasma elimination half-life of 5.6 hours in rabbits. O'Reilly et al. (1963) reported that the mean half-life varied from 24 to 58 hours for disappearance of warfarin from the plasma of human volunteers given a single oral dose of 0.5 to 100 mg ai/kg; no dose-dependent effect on half-life was apparent over this range of doses.

Table 40. Percentage of Diphacinone Retained by Rats Dosed For 1 or 2 Days With 0.32 mg ai/kg (adapted from Diaz and Whitacre 1976)

Organ	% of total dose retained[a]	
	48 h after 1 dose	72 h after 2 doses
Intestine	22.1	4.1
Liver	19.4	5.4
Hide and tail	10.9	6.5
Carcass	3.9	3.8
Blood	1.8	4.0
Muscle	0.8	0.4
Kidney	0.7	0.3
Testis	not reported	0.8
Lung	0.5	0.2
Fat	0.2	0.4
Heart	0.1	0.2
Spleen	0.1	0.1
Brain	<0.1	<0.1

[a] because only 66-70% of the total dose was recovered, percentages in tissues are likely to be higher than the values tabulated

Potential Secondary Risks

Birds

Qualitative assessments of potential secondary risks are based on mortality and other adverse effects reported in secondary-hazards tests, information obtained from field studies and operational control programs, toxicokinetic data, residue levels reported in primary consumers, and incidents. Much of the data are presented in preceding sections of this assessment. It can be difficult to extrapolate from laboratory data to wild birds in the field, because of factors such as animal behavior and environmental conditions. However, laboratory tests are not necessarily overly conservative as argued by some registrants. As discussed in the *Final Report of the Avian Effects Dialogue Group, 1988-1993* (AEDG; Rymph 1994), even sublethal effects seen in controlled laboratory conditions might result in decreased survival or reproduction in the field where animals also are exposed to other stressors, and such effects often are overlooked in the risk assessment process. The AEDG notes that "Decreases in the survival or reproduction of birds following acute or chronic pesticide exposures that would be sublethal in the laboratory may result from alterations in physiological condition, motor function and behavior."

Additional information also is available to demonstrate that exposure to rodenticide baits can have adverse effects. Information from field studies and control program is presented below, and incident data that help characterize secondary risks are discussed in an "*Incident Data: Birds and Nontarget Mammals*" section later in the document. Data gaps exist for some of the rodenticides, but some marked differences in potential secondary risk are apparent among the compounds.

Based on the available feeding studies, brodifacoum poses the greatest potential secondary risk to birds. In 11 secondary-hazard studies that exposed 149 raptors or scavengers to brodifacoum-poisoned prey, 42% of exposed birds died. Many survivors exhibited signs of intoxication, including bleeding. Moreover, mortality via secondary exposure is not limited to laboratory tests but has also been widely reported in field studies and brodifacoum control programs (see below). Brodifacoum residue also has been detected in the liver of numerous dead owls, eagles, hawks, and corvids (see Attachment D). Potential risks of difethialone cannot be adequately characterized until secondary-hazard data are available. However, based on its similarity to brodifacoum in chemical structure (Attachment A), physical and chemical properties, acute toxicity profile for birds (Table 3) and mammals (Table 8), and retention times in animal tissue (Table 34), difethialone is presumed to pose comparable risks. Some uncertainty exists due to the lack of hazard data and also because difethialone baits are formulated with less active ingredient (25 ppm) than are brodifacoum baits (50 ppm).

The other anticoagulants also exhibit a potential for secondary risk to birds but not to the same extent as brodifacoum and possibly difethialone. Secondary hazard studies suggest that bromadiolone and diphacinone pose greater potential risks than do chlorophacinone and warfarin, which are less hazardous and less likely to bioaccumulate in body tissues.

Some information is available for zinc phosphide, but additional data are needed to characterize potential secondary risks of bromethalin and cholecalciferol. Studies indicate that zinc phosphide has a low secondary hazard, probably because it is rapidly converted to phosphine gas in the stomach and not retained in toxicologically significant quantities in body tissues of primary consumers. However, undigested bait in primary consumers may pose a hazard to raptors or scavengers that might consume the GIT.

Based on the data from secondary hazard laboratory studies and the data available on retention times in blood and liver of target species, the comparative analysis model indicates that brodifacoum and difethialone pose the greatest potential secondary risks to birds (Table 41). Brodifacoum has higher summary values than difethialone for all three measures of effect. Mean (%) mortality of secondary lab studies appears to be the most significant measure of effect leading to the conclusion that brodifacoum poses substantially greater potential secondary risk to birds than the other rodenticides (Figure 4).

Table 41. Comparative Analysis Model Results for Secondary Risk to Birds

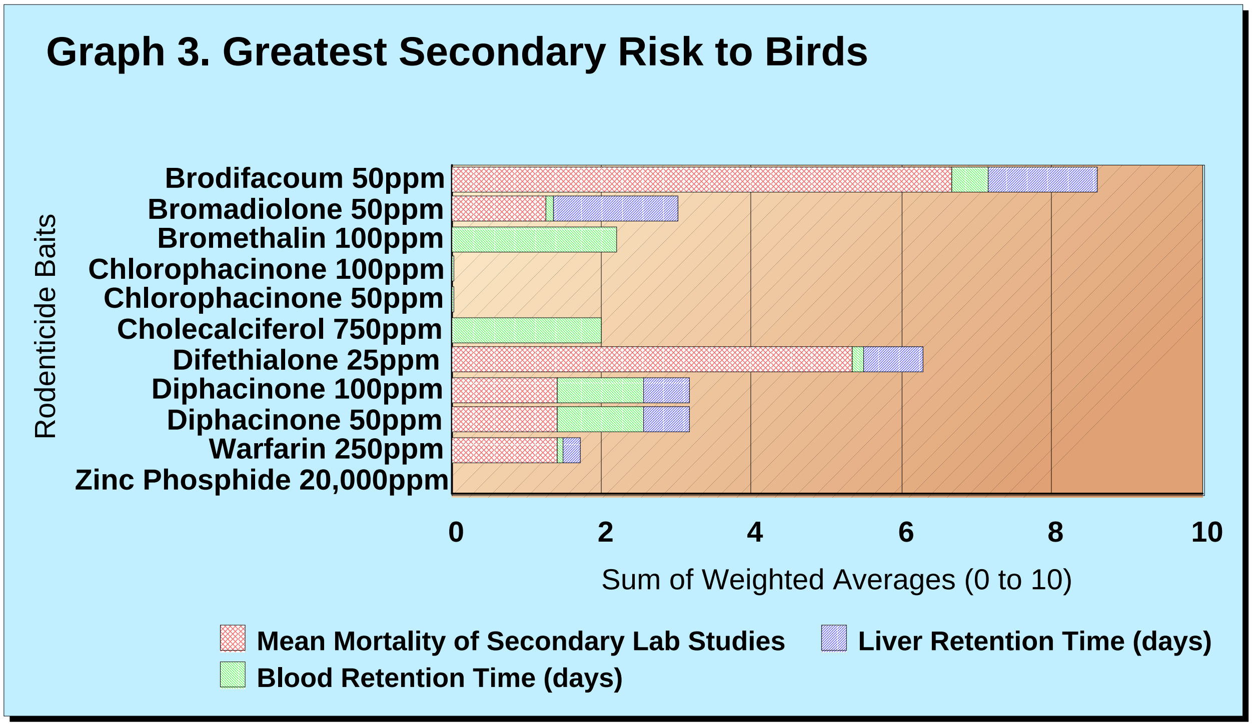
Rodenticide	mg ai/kg bait	Measure-of-effect values			Summary value
		mean mortality (%)[a]	blood retention time (days)[b]	liver retention time (days)[b]	
Brodifacoum	50	42.00	7.30	217.00	8.60
Bromadiolone	50	8.00	1.40	248.00	3.03
Bromethalin	100	No Data	5.60	No Data	2.20
Chlorophacinone	100	0.00	0.40	No Data	0.03
Chlorophacinone	50	0.00	0.40	No Data	0.03
Cholecalciferol	750	0.00	25.50	No Data	2.00
Difethialone	25	33.60[c]	2.50	117.70	6.29
Diphacinone	100	9.00	17.50	90.00	3.18
Diphacinone	50	9.00	17.50	90.00	3.18
Warfarin	250	9.00	0.82	35.00	1.72
Zinc phosphide	20,000	0.00	No Data	No Data	0.00

[a] from Tables 11-12, 14-16, and 18-19

[b] from Tables 13 and 17

[c] as noted in Appendix C, difethialone is considered a special case due to its similarity to brodifacoum; while missing data, it is given a % equal to 80% of that for brodifacoum.

Figure 4. Comparative Analysis Model Summary Values For Secondary Risk to Birds



Information from field studies and control programs: Some information from field studies and control programs is available for some rodenticides, especially brodifacoum. Hegdal and Colvin (1988) examined risk to Eastern screech-owls (*Otus asio*) during experimental baiting for vole control in orchards during the fall and winter of 1981-82. The study indicates considerable risk to screech-owls and possibly other raptors that feed on voles baited with a 10 ppm brodifacoum bait (baits registered for rat and mouse control are 50 ppm). Thirty-two screech-owls were radio-tracked after the baiting. Some owls disappeared or were taken by predators, but the minimum documented mortality of screech-owls was 58% for those individuals for which more than 20% of their home range included treated orchard. Mortality was also considerable (17%) for those owls having less than 10% of their home range including treated areas. Liver-residue analysis was conducted on 16 screech-owls collected or found dead during the study. Although the limit of detection 0.3 ppm was deemed inadequate by the authors, brodifacoum residue was detected at levels ranging from 0.3 to 0.8 ppm in 9 owls., and residue was found in owls collected up to 57 days posttreatment. Death of a long-eared owl (*Asio otus*) also was presumed due to brodifacoum, based on extensive hemorrhage and detection of residue in owl pellets containing vole remains.

Hegdal and Blaskiewicz (1984) found no secondary risk to barn owls residing on New Jersey farms when brodifacoum was applied to control rats and mice from late July to September in 1980. Radio-telemetry data for 34 owls indicated they spent most feeding time hunting for meadow voles in fields and marshes and spent little time foraging for rats and mice around farms. Rats and mice comprised only 3.9% and 2% of the diet, respectively, and owl traps baited with mice and placed around farmsteads were ignored by owls. In contrast, Duckett 1984 (cited in Newton et al. 1999 and Eason and Spurr 1995) reported a major decline in a barn owl population on an oil palm plantation in Malaysia after second-generation anticoagulants were applied for rat control. The owls were feeding on rats and the owl population declined from 40 to 2 individuals.

Howald et al. (1999) examined effects of brodifacoum baiting on avian scavengers during rat control on a Canadian island. They conclude that there is a very real risk of secondary poisoning of some predators and scavengers, and the impact on ravens may have been severe. Thirteen dead ravens were found out of an island population estimated at 20 to 72 individuals. All 13 dead ravens had brodifacoum residue in the liver, with concentrations ranging from 0.98 to 2.52 ppm. Ravens were likely exposed from eating the bait as well as secondarily via prey who had previously fed on the bait. Secondary poisoning is evident from observations of ravens scavenging on rat carcasses and the presence of rat hair in the gizzard of several ravens. Assuming an LD50 of 0.56 mg ai/kg (a value offering 95% species protection for birds) and a rat total-body burden of 1.4 mg ai (based on measured residue concentrations in 10 rats), the authors calculate that a single brodifacoum-poisoned rat could provide 2 to 3 LD50 doses for a raven or crow. No mortality of bald eagles was evident during the baiting program, but exposure occurred. Twenty bald eagles were trapped and 1 other rescued during the baiting program. Brodifacoum was detected at levels of 0.037, 0.041, and 1.74 ppm in the blood plasma of 3 (15%) of 21 eagles sampled. The authors calculated that a bald eagle, because of its large size, would need to eat about 3.2 rats to obtain an LD50 dose.

Based on numerous bird kills during operational control programs with brodifacoum in New Zealand, Eason and Spurr (1995) conclude that the potential for secondary adverse effects is much greater for second-generation anticoagulants than for first-generation anticoagulants. Secondary adverse effects on Australasian harriers (*Circus approximans*), New Zealand falcons (*Falco novaeseelandiae*), rails, brown skuas (*Catharacta skua*), gulls, and owls (morepork, *Ninox novaeseelandiae*) has been reported after brodifacoum baiting (Eason and Spurr 1995, Towns et al. 1993, Ogilvie et al. 1997, Walker and Elliott 1997). Stephenson et al. (1999) studied the fate of moreporks, which feed on mice, after a single aerial application of brodifacoum to eradicate mice on Mokoia Island. Twenty-eight owls were monitored after the baiting, including 14 that were radio-tagged and tracked. Three (21%) radio-collared owls died. Seven (50%) owls not radio-collared disappeared, which the authors believe is most likely a result of secondary poisoning. Two dead owls were analyzed for residue, and brodifacoum was detected in the liver of both at concentrations of 1 and 1.1 ppm.

A survey in Great Britain indicates that exposure of barn owls to second-generation anticoagulants may be frequent and widespread. As part of a pesticide-monitoring scheme, the livers from 717 dead barn owls were analyzed for anticoagulant residue from 1983 to 1996

(Newton et al. 1990, 1999; Wyllie 1995). Although second-generation anticoagulants were detected in 26% of the owls (34 to 37% in the latter years when better analytical methods were available), most deaths resulted directly from collisions with cars and trucks or starvation. However, the authors believe that the proportion of deaths due to rodenticides may have been underestimated. Almost all carcasses had been collected from open areas, such as roadsides. As the authors note, death from anticoagulant exposure is delayed and preceded by lethargy, and most victims are likely to die in their roosts, in roof-cavities or hollow trees, where they are not likely to be found. Also, carcasses found in such locations are most often too decayed to permit tissue analysis. Newton et al. (1990) also note that ". . . there remains the possibility that sub-lethal levels of rodenticide may predispose death from other causes, or reduce the chance of recovery from accidents.", and they emphasize that ". . . more monitoring of residues and population trends is clearly desirable."

No field studies are available for difethialone or bromadiolone. Some information on nontarget exposure to bromadiolone has been reported in France and Switzerland, where bromadiolone is used for control of water voles (*Arvicola terrestris*) and coypu (nutria). From 1991 to 1994, a number of dead birds suspected to have been exposed to anticoagulant rodenticides were submitted for analysis. Bromadiolone was detected in the liver of 15 of 16 dead Eurasian buzzards, 5 of 5 kites (*Milvus migrans*), and the one harrier examined (Berny et al. 1997). Saucy et al. (2001) reported deaths of numerous birds, mostly Eurasian buzzards but also kites and carrion crows, after bromadiolone bait (150 ppm) was mechanically applied in underground burrows for water vole control in Switzerland.

The Agency is not aware of any field tests designed to assess secondary risk to raptors from first-generation anticoagulants or the non-anticoagulants. Several field tests designed to assess the efficacy of chlorophacinone and zinc phosphide included searches for nontarget carcasses as a secondary objective. None found any indications that raptors or avian scavengers were killed from feeding on target species previously exposed to the rodenticides. However, most search effort was devoted to locating nontarget carcasses on and immediately around baited plots. Because raptors may be wide-ranging and anticoagulants are slow-acting, radio-tracking individual birds is essential to evaluate their interactions with the target species and to determine their fate (Fagerstone and Hegdal 1998, Colvin et al. 1991, Colvin et al. 1988, Edwards et al. 1988).

Nontarget mammals

Based on a qualitative assessment of potential secondary risk to mammals from feeding studies, all 6 anticoagulants appear to pose a potential secondary risk to mammalian predators and scavengers, although warfarin apparently less so than the others. Secondary risks from zinc phosphide appear to be low for most species, especially those that don’t consume the GIT where undigested bait may be present. Too few data are available to adequately assess potential risks of either bromethalin or cholecalciferol.

The comparative analysis model results indicate that diphacinone, chlorophacinone, and brodifacoum pose the greatest potential secondary risk to mammals (Table 42). Retention time in blood was the most significant measure of effect leading to the conclusion that diphacinone poses greater potential secondary risk than does chlorophacinone, while mean (%) mortality of secondary lab studies was the most significant measure of effect leading to the conclusion that both diphacinone and chlorophacinone poses greater potential secondary risk than does brodifacoum (Figure 5).

Table 42. Comparative Analysis Model Results for Secondary Risk to Mammals

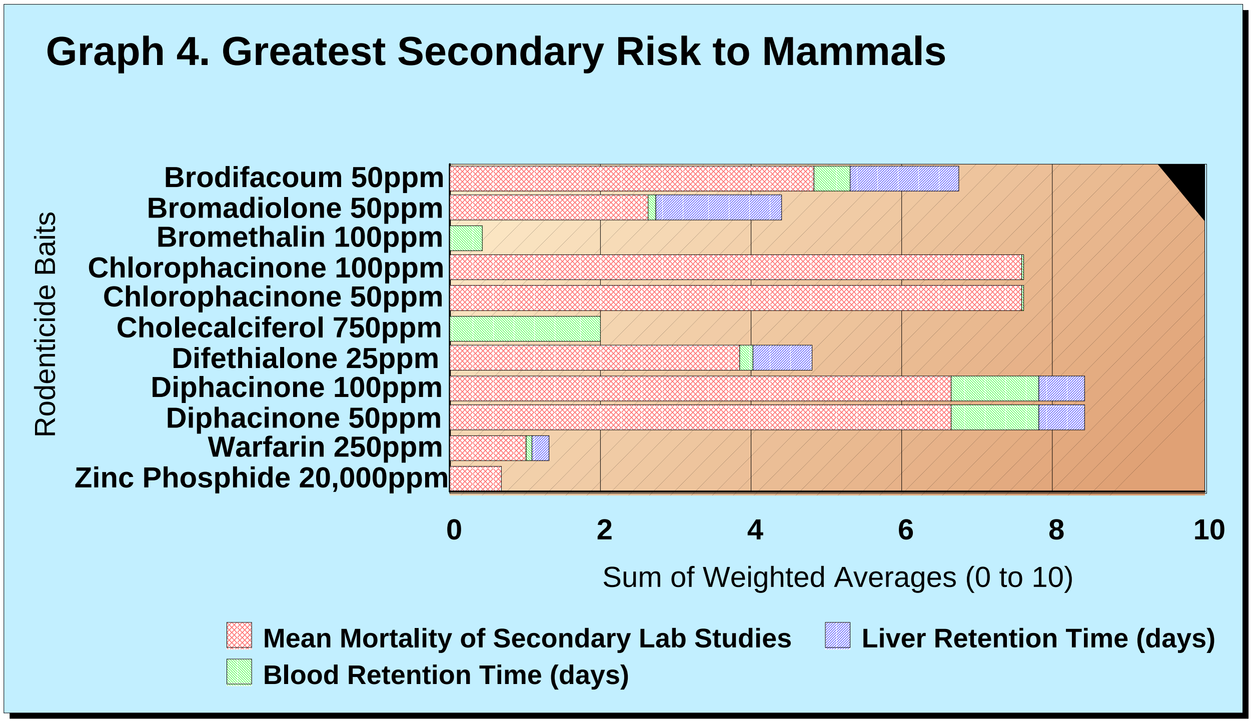
Rodenticide	mg ai/kg bait	Measure-of-effect values: mean mortality (%)[a]	blood retention time (days)[b]	liver retention time (days)[b]	Summary value
Brodifacoum	50	42.00	7.30	217.00	6.76
Bromadiolone	50	23.00	1.40	248.00	4.40
Bromethalin	100	0.00	5.60	No Data	0.44
Chlorophacinone	100	55.00	0.40	No Data	7.62
Chlorophacinone	50	55.00	0.40	No Data	7.62
Cholecalciferol	750	0.00	25.50	No Data	2.00
Difethialone	25	33.60[c]	2.50	117.70	4.82
Diphacinone	100	58.00	17.50	90.00	8.42
Diphacinone	50	58.00	0.82	90.00	8.42
Warfarin	250	9.00	5.60	35.00	1.32
Zinc phosphide	20,000	4.00	No Data	No Data	0.69

[a] from Tables 20-27

[b] from Tables 13 and 17

[c] as noted in Appendix C, difethialone is considered a special case due to it's similarity to brodifacoum; while missing data, it is given a % equal to 80% of that for brodifacoum.

Figure 5. Comparative Analysis Model Summary Values For Secondary Risk to Nontarget Mammals



Information from field studies and control programs: The Agency is not aware of any field studies designed to assess secondary risks to mammals, but exposure and mortality has been documented in some situations. Extensive mortality of introduced mammalian predators was reported during brodifacoum-baiting operations for rats in New Zealand forests. Mortality of stoats (ermine), ferrets, weasels, and cats was reported to be 100% after brodifacoum application (Alterio 1996, Alterio et al. 1997; cited in Stephenson et al. 1999). In one study, all 11 radio-collared stoats and the 1 radio-collared weasel died within 9 days of bait application. In another study, Murphy et al. (1998) detected brodifacoum residues in the liver of 56% of 16 feral ferrets, 78% of 40 stoats, and 71% of 14 weasels examined after baiting.

Some information on nontarget exposure of mammals to bromadiolone was obtained during vole and coypu control in France (Berny et al. 1997). Bromadiolone was detected in the liver of 22 of 31 red foxes (*Vulpes vulpes*), 4 of 28 rabbits (*Oryctolagus cuniculus*) and hares (*Lepus capensis*), 3 of 6 wild boar (*Sus scrofa*), 2 roe deer (*Capreolus capreolus*), 2 stone martens (*Martes foina*), a lynx (*Lynx lynx*), and a badger (*Meles meles*). Based on the species involved, secondary poisoning seems to have been the predominant route of exposure. Saucy et al. (2001) reported deaths of 38 wild mammals, mostly red foxes and mustelids, and 18 cats and dogs after bromadiolone bait (150 ppm) was mechanically applied in underground burrows for water vole control in Switzerland.

Second-generation anticoagulants were detected in the liver of 31% of 29 polecats (*Mustela putorius*) analyzed from 1992 to 1994 in Britain (Shore et al. 1996, Newton et al. 1999). Most of the carcasses collected were found along roadsides. The authors believe the survey results indicate exposure of polecats to second-generation rodenticides may be common, and they suggest that studies to determine potential effects of such exposure are warranted.

Savarie et al. (1979) orally dosed 10 wild coyotes with diphacinone, with doses ranging from 0.31 to 5 mg ai/kg. Radio collars were attached to these animals, and they were released back into the wild and monitored for survival. Seven (70%) of the 10 coyotes died within 7 to 16 days, with an average time to death of 9.6 days.

Incident Data: Birds and Nontarget Mammals

Ecological Incidents Information System (EIIS)

Incident reports submitted to the Agency indicate that birds and nontarget mammals are being exposed to rodenticides, especially brodifacoum. EFED’s EIIS contains information on more than 300 incidents in which one or more of the rodenticides was detected in birds or nontarget mammals (Table 43 and Attachment D). Brodifacoum was detected in more than 244 of those, including 25 of 26 involving exposure to more than one rodenticide. Bromadiolone was detected in 39 incidents, including 17 that also involved exposure to brodifacoum. Twenty-five incidents are reported for zinc phosphide, 20 for diphacinone, 13 for chlorophacinone, 4 for warfarin, 1 for difethialone, and none for bromethalin or cholecalciferol. Eleven of the incidents for the first-generation anticoagulants also included exposure to a second-generation anticoagulant, usually brodifacoum. Approximately 80 additional incidents involving raptors exposed to anticoagulant rodenticides, mostly brodifacoum (84%), have been reported by Stone et al. (2003). The New York State Department of Environmental Conservation has committed to providing those incident reports to EFED, and they will be added to the EIIS database when received.

Other anticoagulant-rodenticide incidents in the EIIS include rodents (mostly tree squirrels), opossums, and deer. Seven deer in New York state tested positive for anticoagulants, including 5 with brodifacoum and 2 with diphacinone. The deer apparently were exposed due to misuse and careless bait application.

Zinc phosphide was implicated in the deaths of some wild turkeys, waterfowl (especially geese) and a few squirrels and a rabbit. In most incidents, treated bait was present in crop or gizzard contents. Two red foxes also apparently died after eating mice who fed on zinc phosphide treated grain.

Table 43. Comparative Number of Reported Rodenticide Nontarget Incidents[a]

Rodenticide	Total[b]	Owls	Diurnal raptors	Corvids	Other birds	Wild canids	Wild felids	Other carnivores	Deer	Rodents/ Rabbits	Opossum
Second-generation anticoagulants											
Brodifacoum	244[c]	54	68	17	4	48	5	10	5	31	2
Difethialone	1	0	0	0	0	0	1	0	0	0	0
Bromadiolone	39	13	5	1	2	5	1	3	0	8	1
First-generation anticoagulants											
Chlorophacinone	13	0	1	0	2	5	1	0	0	4	0
Diphacinone	20	3	2	0	1	4	1	2	2	5	0
Warfarin	4	1	2	0	0	0	0	0	0	1	0
Others (non-anticoagulants)											
Bromethalin	0	0	0	0	0	0	0	0	0	0	0
Zinc Phosphide	25	0	0	0	22	1	0	0	0	2	0
Cholecalciferol	0	0	0	0	0	0	0	0	0	0	0

[a] based on confirmed exposure (e.g., detection of anticoagulant in the liver, zinc phosphide in crop contents); see Attachment B for additional details

[b] 26 incidents involved exposure to more than 1 registered anticoagulant

[c] Syngenta reported two incidents in 6(a)(2) aggregate reports; the species and number of individuals involved were not reported for these incidents

Most of the incidents in the EIIS occurred in New York and California, where state agencies have taken the time, effort, and expense of screening the liver of dead animals suspected to have been killed by rodenticides. Few other states appear to do so, although Wisconsin has reported several raptor incidents. A proper evaluation of rodenticide exposure requires necropsy of a dead animal by a wildlife pathologist. Liver tissue be extracted, frozen, and shipped to an analytical laboratory for analysis by high performance liquid chromatography (HPLC). Because so few anticoagulant screens are conducted, exposure of birds to anticoagulants is likely much more widespread than the number of incidents suggests. Most rodenticide incidents likely go undetected except in those rare instances when a predator carcass happens to be exposed in an open area (e.g., roadside) where it is observed by someone willing to take the time and effort to report it to the proper authorities (McDonald et al. 1998, Newton et al. 1999). In many situations, carcasses might not be detected, death may be attributed to natural mortality, or an incident may not be reported for a variety of reasons, including ignorance, apathy, or failure of authorities to investigate and confirm the cause of death (Rymph 1994, Vyas 1999).

The incidents reported in the EIIS are based on confirmed exposure to a rodenticide. Anticoagulants are detected from residue analysis of liver tissue, supplemented by gross pathological findings. According to Stone et al. (1999), the most frequent pathological signs observed in birds (>50% of individuals examined) exposed to anticoagulants are subcutaneous hemorrhage and overall pallor. Occasional signs (10 to 50% of individuals) include inter/intra-muscular hemorrhage, free hemorrhage in the body cavity, excessive bleeding from minor wounds, and low blood volume in the heart and major blood vessels. Toxicosis resulting from exposure to non-anticoagulants may be more difficult to confirm than for an anticoagulant. Zinc phosphide is generally detected by the presence of dyed bait in the crop, stomach, or alimentary canal. The presence of an acetylene odor also is diagnostic of zinc phosphide toxicity but can be detected only if intact carcasses are sent to an examining laboratory soon after death (Michigan Wildlife Diseases Manual, undated). Little information is available on methodology for detecting bromethalin or cholecalciferol in body tissues.

Anticoagulant rodenticides, especially brodifacoum, have been detected in numerous predators and scavengers. Avian species most commonly exposed are great horned owls and red-tailed hawks. Multiple incidents also have been reported for golden and bald eagles, corvids, barn owl, eastern screech-owl, northern spotted owl, Cooper’s hawk (*Accipiter cooperii*), red-shouldered hawk, sharp-shinned hawk (*Accipiter striatus*), peregrine falcon (*Falco peregrinus*), American kestrel, and vultures. Other incidents have included a long-eared owl, a barred owl (*Strix varia*), a snowy owl (*Nyctea scandiaca*), and a spotted owl (*Strix occidentalis*). Carnivores exposed include coyotes, various foxes (including the endangered kit fox), raccoons, bobcats, skunks, mountain lions, and a weasel. Brodifacoum was detected most often, followed by bromadiolone, chlorophacinone, and diphacinone. Difethialone was detected in 1 dead bobcat.

The American Society for Prevention of Cruelty to Animals (ASPCA) Poison Control Center also has some incident information for pets, mostly dogs. The Center reports 2334 cases involving potential exposure of 2685 animals from November 01, 2001 to June 16, 2003 (S. Hansen, Senior Vice President, pers comm.). By rodenticide, the number of cases were 1161 for brodifacoum, 511 for bromadiolone, 218 for zinc phosphide, 206 for diphacinone, 66 for bromethalin, 48 each for difethialone and warfarin, 42 for chlorophacinone, and 34 for cholecalciferol. EFED does not assess risks to pets, and these data are not a component of the EIIS. However, they do augment the wildlife incident data in demonstrating that nontarget animals are being exposed to some rodenticides, despite product-label use directions to apply bait in locations out of reach of children, pets, domestic animals and nontarget wildlife, or in tamper-resistant bait stations.

The Rodenticide Registrants Task Force (Kaukeinen et al.2000) believe that rodenticide incidents are few when compared to other sources of wildlife mortality. They note that diseases accounted for most of the mortality reported by the National Wildlife Health Center (NWHC) from July 1998 through March 1999 and that there is only a single rodenticide incident. This is not surprising, because the NWHC focuses on diseases and does not analyze wildlife carcasses for rodenticide residues (A. Schrader, NWHC, pers comm.). The Rodenticide Registrants Task Force also contend that bird deaths from collisions with television and radio towers, starvation, and parasitism far exceed deaths attributable to rodenticides. However, small birds such as sparrows, starlings, and other songbirds far outnumber predatory birds such as owls, hawks, and eagles in such incidents. The latter are more likely to comprise incidents attributed to rodenticide toxicity and are more likely to be found and reported. Based on an analysis of the EIIS by Mastrota (1999), brodifacoum was surpassed only by diazinon in the number of wildlife incidents reported for pesticides from 1994 through 1998, the latest period analyzed.

New York State Raptor Incidents

Stone et al. (1999, 2003) provide some perspective on the extent of exposure on some raptor species. They reported 26 cases of anticoagulant poisoning of raptors in New York State from 1994 to 1997, of which 23 (88%) involved brodifacoum. The incidents comprised 17% of all diagnoses for great horned owls (n = 59) and 6% of all diagnoses (n = 114) for red-tailed hawks during that period. For the period 1998 through 2001, they detected anticoagulant rodenticide in 49% of the 265 raptors analyzed in New York State (Table 44). Brodifacoum was detected in 84% of the positive cases and bromadiolone in 22%. One or more anticoagulants were detected in 12 of 19 species examined, with most detections made in great horned owls (81%), red-tailed hawks (58%), Cooper’s hawks (36%), and screech owls (45%). Mean residue levels in those 4 raptor species are presented in Table 45. The data are not sufficient to determine if these exposures are impacting local or state-wide populations of these species via mortality or reduced reproductive success, but they do indicate a need for a sound monitoring program to determine potential adverse effects of such exposure.

Table 44. Detection of Anticoagulant Rodenticides in Liver Tissue of Raptors and Vultures In New York State From 1998 Through 2001 (from Stone et al. 2003)

Species	no. analyzed	no. with anticoagulant rodenticide	% positive detects
Red-tailed hawk	78	45	58
Great horned owl	53	43	81
Cooper’s hawk	50	18	36
Screech owl	22	10	45
Barred owl	13	3	23
Long-eared owl	7	2	29
Turkey vulture	2	2	100
Golden eagle	1	1	100
Bald eagle	5	1	20
Sharp-shinned hawk	11	1	9
Saw-whet owl	3	1	33
Peregrine falcon	2	1	50
Broad-winged hawk	11	0	0
Snowy owl	2	0	0
Northern goshawk	1	0	0
Rough-legged hawk	1	0	0
Merlin	1	0	0
Short-eared owl	1	0	0
Black vulture	1	0	0

Table 45. Anticoagulant Rodenticide Residues In Four Raptor Species Analyzed by Stone et al. (2003)

Anticoagulant/ Raptor species	no. detects	0 liver residue (ppm)	liver residue range (ppm)
Brodifacoum:			
Red-tailed hawk	42	0.21	0.006-1.28
Great horned owl	42	0.21	0.007-0.97
Screech owl	8	0.16	0.007-0.47
Cooper's hawk	12	0.10	0.008-0.22
Bromadiolone:			
Red-tailed hawk	6	0.23	0.08-0.50
Cooper's hawk	5	0.35	0.04-0.60
Diphacinone:			
Red-tailed hawk	1	0.34	
Cooper's hawk	1	0.10	
Warfarin:			
Great horned owl	1	0.73	
Cooper's hawk	1	0.10	
Chlorophacinone:			
Red-tailed hawk	1	0.18	

Endangered San Joaquin kit fox

Of particular concern are findings over the past several years that the endangered San Joaquin kit fox is being exposed to rodenticides, especially brodifacoum. From 1999 to 2003, liver tissue from 32 dead kit foxes has been screened for rodenticide residues by the Pesticide Investigations Unit of the California Department of Fish and Game and by the U. S. Fish and Wildlife Service (R. Hosea, pers. comm.). Anticoagulant rodenticide was detected in the liver of 27 (84%) foxes. Brodifacoum was detected in all 27 individuals. Bromadiolone also was detected along with brodifacoum in 2 of those foxes, and chlorophacinone and pival were found with brodifacoum in 1 fox each. Pival is no longer registered but may have been used under existing-stocks provisions.

Liver residue levels

Uncertainty exists as to what liver concentration might corroborate death or other adverse effects from anticoagulant exposure or even if such a cause-effect relationship is appropriate. The Rodenticide Registrants Task Force proposes a "threshold of toxicity" of 0.7 ppm for brodifacoum in liver tissue (Kaukeinen et al. 2000, Anonymous 2001). However, the proposed threshold level is based on only 2 laboratory studies with a total of 8 barn owls and some selected field surveys. Variation in susceptibility of different bird species, mammals, and other rodenticides is not addressed. Brodifacoum concentrations less than 0.7 ppm have been associated with toxicosis. Eason et al. (1996), for example, dosed 6 brushtail possums with a dose of 0.1 mg ai/kg and reported that 1 animal that died had a liver concentration of only 0.1 ppm brodifacoum. In another study, possums were offered brodifacoum baits for 3 nights (C. Eason, pers comm.). Mean bait consumption of 165.1 g, equivalent to 0.86 ± 0.04 mg ai/kg brodifacoum (range 0.33 to 1.09 mg ai/kg), provided a lethal dose. Extensive hemorrhaging was observed. The mean concentration in the liver was 0.56 mg ai/kg (range 0.17 to 1.04 mg ai/kg), and most animals that died had a liver concentration below the Rodenticide Registrants Task Force's proposed threshold level of 0.7 mg ai/kg. Hegdal and Colvin (1988) collected dead screech-owls during a brodifacoum-baiting study in Virginia; 8 of 9 dead owls with detectable residue had a level <0.7 ppm, and most had hepatic concentrations ranging from 0.3 (the limit of detection) to 0.5 ppm. Those authors also note that other wildlife has been killed in which brodifacoum liver residues were as low as 0.05 ppm (e.g., Rammell et al. 1984). Brown et al. (1996), in their review entitled "*Identification of pesticide poisoning in wildlife*", state that anticoagulant residues remaining after death are usually above or around 0.1 ppm.

A recent incident in Georgia correlates low levels of liver residue with deaths of a red-tailed hawk and a barn owl. These birds and several other raptors were housed in mews at the Amicalola Falls State Park. In November of 2003, the hawk and owl began showing abnormal physical and behavioral symptoms, and both birds died within a few days. Two other great horned owls later showed similar symptoms and were treated with vitamin K. A dead rat was also discovered in a hole in the back of one of the raptor cages. Second-generation anticoagulant rodenticides were in used at the park at the time of the incident to control rats around a lodge and intern housing. Necropsy of the bird carcasses by the Southeastern Cooperative Wildlife Disease Study, The University of Georgia, found moderate to severe clavarial hemorrhage in both birds and moderate focal myocardial hemorrhage in the barn owl. Microscopic examination also showed moderate to severe multifocal hemorrhage in the owl. Microbiological tests were negative. A fresh liver and kidney samples from each bird were screened for heavy metals and organic chemicals, including anticoagulant rodenticides. The only chemical detected in either bird was brodifacoum, with concentrations measured in the at 0.077 ppm in the hawk and 0.007 ppm in the owl. Despite the very low levels detected, the evidence of this case strongly indicates that the birds died from secondary poisoning by feeding on rats exposed to brodifacoum.

Hosea et al. (2001) demonstrate the importance of a proper necropsy in a case where a low liver-residue concentration (0.04 ppm) in the liver determined that brodifacoum caused the death of a golden eagle in California:

> "The carcass of an adult Golden Eagle was recovered from its breeding territory in Contra Costra County on March 11, 1999 (DFG case accession # P-2060A). The bird had been part of a long term radio telemetry study of eagles in the area. Based on telemetry data the breeding territory consisted mainly of open rangeland and random outbuildings with some areas of urban development.
>
> "The bird was not recovered in the vicinity of power lines and the feathers did not have the "singed" odor characteristic of accidental electrocution. The necropsy indicated no other evidence of physical trauma. The animal was skinned to determine the presence of puncture wounds from conflicts with other eagles or from a gunshot. The pericardial sac contained serum and blood. Approximately 65% of the surface of the heart muscle was haemorrhagic. The major vessels associated with the heart contained unclotted blood. The lung tissue was haemorrhagic, bleeding from a cut surface. the cerebro-spinal fluid was blood stained, indicating cranial haemorrhage. These clinical signs were consistent with previously published symptoms of anticoagulant toxicosis in raptors (Hegdal et al. 1988, Mendenhall and Pank 1980, Newton et al. 1990, Radvanyi et al. 1988). Liver tissue was analyzed for residues of anticoagulant rodenticides. Kidney tissue was also analyzed for lead concentrations. Kidney tissue had a lead concentration of 1.1 ppm, well below the level that would indicate acute toxicosis (Aiello 1998). Liver tissue had a brodifacoum concentration of 0.04 ppm. The presence of the rodenticide in liver tissue alone does not support a diagnosis of anticoagulant toxicosis. However, if considered in conjunction with the observed clinical signs consistent with anticoagulant toxicosis, a diagnosis of anticoagulant toxicosis is supported."

C. Eason (pers comm.) provided data depicting the range of brodifacoum concentration in various birds collected dead in areas where brodifacoum was applied in New Zealand. A total of 66 (63%) out of 105 birds found dead and 33 (40%) out of 82 collected alive contained brodifacoum residue (Table 44). As might be expected, brodifacoum residues were found in higher concentrations in birds found dead than in birds collected alive. Many dead birds had a liver concentration <0.7 ppm.

Taken together, findings from the field and the incident data indicate that the liver is an appropriate organ for determining exposure of birds and mammals to anticoagulant rodenticides. However, establishing a toxicity threshold of 0.7 ppm seems to be inappropriate and is not supported by the available data on mortality. Moreover, a toxicity threshold would need to account for adverse sublethal effects (e.g., reproductive, chronic).

Table 44. Brodifacoum Residues Detected In the Liver of Birds In New Zealand (compiled by C. Eason; data obtained from the New Zealand National Vertebrate Pesticide Database and Towns et al. 1994, Morgan et al. 1996, Ogilvie et al. 1997, Dowding et al. 1999, Empson and Miskelly 1999, Robertson et al. 1999, and Stephenson et al. 1999)

Species	Collected alive				Collected dead			
	No. tested	No. positive	mg ai/kg in positives		No. tested	No. positive	mg ai/kg in positives	
			mean	range			mean	range
Astralaian harrier	1	0			2	2	0.64	0.61-0.66
Australasian magpie	10	2	0.25	0.08-0.41	10	2	0.47	0.08-0.99
Bellbird	1	0						
Blackbird	6	6	0.10	0.01-0.20	7	7	0.55	0.01-1.10
Chaffinch					3	3	1.43	0.12-2.31
Paradise shelduck					4	4	0.56	0.24-0.80
Grey duck					1	1	0.91	
Mallard					2	2	1.07	0.90-1.23
Fantail	1	0						
Kaka (parrot)					3	3	2.87	1.20-4.10
Kakariki (parakeet)					2	1	0.03	
Kereru (pigeon)					5	0		
Brown kiwi					29	14	0.09	0.01-0.69
Kokako (wattlebird)					4	0		
Morepork (owl)	1	1	0.61		3	3	1.84	0.97-3.44
Myna					3	3	0.80	0.54-1.27
Pukeko (gallinule)					8	8	0.86	0.52-1.35
Robin, Chatham Island					1	1	0.35	
Robin, North Island					1	1	0.58	
Saddleback					4	2	0.33	0.05-0.60

	Collected alive				Collected dead			
			mg ai/kg in positives				mg ai/kg in positives	
Species	No. tested	No. positive	mean	range	No. tested	No. positive	mean	range
Silvereye					1	0		
Southern black-backed gull					1	1	0.58	
Spotless crake					1	1	0.04	
Tomtit	5	0			1	0		
Tui (honeyeater)					1	0		
Weka (rail)	48	24	0.25	0.01-0.95	7	7	1.08	0.11-2.30
Whitehead	5	0			1	0		

The liver is only one of many organs and tissues in which anticoagulant residue accumulates in the body. Concentrations in the liver are often, but not always, higher than in other tissues (e.g., Tables 39, 40, 46, 47). However, because the liver comprises only about 4 to 7% of the weight of a rat or mouse (Newton et al. 1990, Howald et al. 1999), most residue actually may be stored in other parts of the body. For example, Newton et al. (1990) reported a much higher mean residue concentration in liver (2.13 ppm) than in the remainder of the carcass (0.36 ppm) of 10 mice fed brodifacoum bait. However, the mean total amount of residue in the carcass (excluding the liver) was 11.85 µg ai versus only 3.51 µg ai in the liver (Table 47).

Table 46. Tissue Residues in Nine Captive Coyotes Killed With a Single Oral Dose of Diphacinone (adapted from Savarie et al. 1979)

Dose (mg ai/kg)	Tissue residue (ppm)					
	liver	small intestine	kidney	heart	muscle	fat
10	1.2	1.8	0.6	0.5	0.2	<0.1
10	0.7	0.3	0.5	0.2	<0.1	0.3
5	1.8	4.7	1.7	1.5	0.7	<0.1
5	0.5	0.4	<0.1	<0.1	<0.1	<0.1
2.5	0.6	1.3	0.9	0.5	<0.1	<0.1
2.5	0.6	1.0	0.6	0.2	<0.1	<0.1
1.25	1.1	0.5	0.7	0.2	<0.1	<0.1
0.63	1.0	0.3	0.5	0.1	<0.1	<0.1
0.63	0.6	0.2	0.2	<0.1	<0.1	<0.1

Table 47. Brodifacoum Residue in the Liver and Carcass of Mice Fed 20 ppm Bait For 1 Day (adapted from Newton et al. 1990)

Mouse	Liver		Carcass minus liver	
	µg ai	ppm (µg ai/g)	µg ai	ppm (µg ai/g)
1	0.14	0.07	15.39	0.45
2	1.73	1.66	16.07	0.53
3	4.06	3.03	13.13	0.42
4	4.44	2.39	7.44	0.22
5	5.52	2.70	5.10	0.16
6	1.69	1.10	14.48	0.47
7	5.67	3.64	9.77	0.28
8	6.72	2.85	19.83	0.58
9	2.70	1.86	5.37	0.18
10	2.44	1.97	11.88	0.35
mean	3.51 ± 0.66	2.13 ± 0.33	11.85 ± 1.54	0.36 ± 0.05

The "threshold of toxicity" concept (Kaukeinen et al. 2000, Anonymous 2001) also assumes that mortality is the only endpoint of concern. A sublethal dose of anticoagulant can produce significant clotting abnormalities and some hemorrhaging (Eason and Murphy 2001), and such effects might be especially detrimental if combined with other stressors that have additive or synergistic adverse effects. Jaques (1959) reported that stress is a hemorrhagic factor in rabbits and rats, and it could be induced by a variety of factors (e.g., frostbite, insulin, NACL). Only 6% of his rats died after 5 days of exposure to an anticoagulant compound (dicoumarol), but 50% died when exposed to the anticoagulant and additional stressors. Others have speculated that birds exposed to anticoagulants may become more susceptible to environmental stressors, such as adverse weather conditions, food shortages, and predation (Hegdal 1985, Hegdal and Colvin 1988, LaVoie 1990). Newton et al. (1999) have speculated that sublethal levels of rodenticide might predispose death from other causes (e.g., collisions with automobiles, starvation) or may reduce the chance of recovery from accidents.

Three golden eagles (*Aquila chrysactos*) recently died in captivity during relocation from the California Channel Islands (J. Linthicum, The Santa Cruz Predatory Bird Research Group [TSCPBRG], pers. comm.). Necropsies were performed and tissues analyzed for a variety of contaminants. Hemorrhaging in lung and brain tissue was reported in 2 birds, and brodifacoum was detected in the liver (0.004 to 0.026 ppm) of all 3 birds. TSCPBRG has trapped hundreds of golden and bald eagles as part of various studies and never previously had an injury or fatality. SCPBRG noted that "Birds of prey, in particular golden eagles, are hardy, tough animals." and

"Nothing in our experience or other's we have spoken to suggest that these birds should have died under these circumstances." Brodifacoum can't be directly implicated in the deaths of the 3 golden eagles, but concern exists. These birds might have succumbed to brodifacoum when augmented by additional stresses from handling and captivity.

Papworth (1959), in discussing the mechanism of anticoagulant toxicity, speculated that a slight scratch, bruise, or even a minor internal injury might lead to death from hemorrhage if clotting is inhibited over an injured surface. Some incidents reported to the Agency suggest that raptors exposed to anticoagulants can be in danger of excessive bleeding from minor wounds caused by their prey. Such wounds, not normally life-threatening, may cause prolonged bleeding and mortality when blood-clotting mechanisms are disrupted. One great horned owl exposed to brodifacoum (0.64 ppm liver residue) was collected near death on a farm where brodifacoum bait had been applied in barns and sheds. This owl was almost completely exsanguinated from a small laceration on a toe. Other owls and hawks found dead had bled excessively from minor wounds, usually on their feet, likely inflicted by prey (see Attachment D). A partially eaten muskrat was found by one dead owl that appeared to have bled excessively from a puncture wound extending from between the eyes into the sinuses. Brodifacoum was detected in the liver of these raptors at concentrations ranging from 0.08 to 0.80 ppm. Bromadiolone also was detected in 1 owl.

Some of the concerns and uncertainties regarding possible adverse sublethal effects can be addressed through avian reproduction studies, which the Agency will require for all pesticides with outdoor uses. The no-observable-adverse-effects concentration (NOAEC) established from these studies will be a more appropriate indicator of a toxicity threshold than is the liver residue in dead animals.

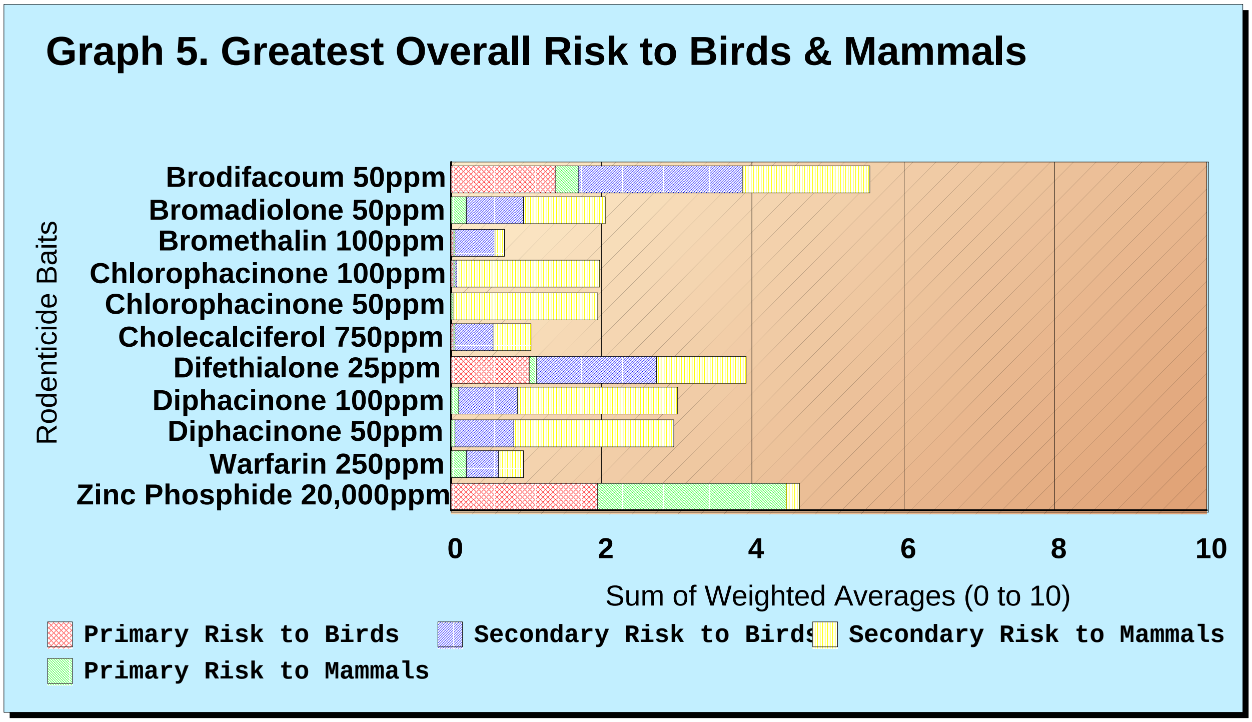
Conclusions

The available information indicates that differences exist among these rodenticides in their potential risks (primary and secondary) to birds and nontarget mammals. Based on the comparative analysis model, comparing measures of effect for primary and secondary risks to birds and mammals, brodifacoum, zinc phosphide, and difethialone are ranked as the rodenticides posing the greatest potential overall risk (Table 48, Figure 6).

Table 48. Comparative Analysis Model Results for Overall Risk to Birds and Mammals. Tabulated values are weighted measures of effect.

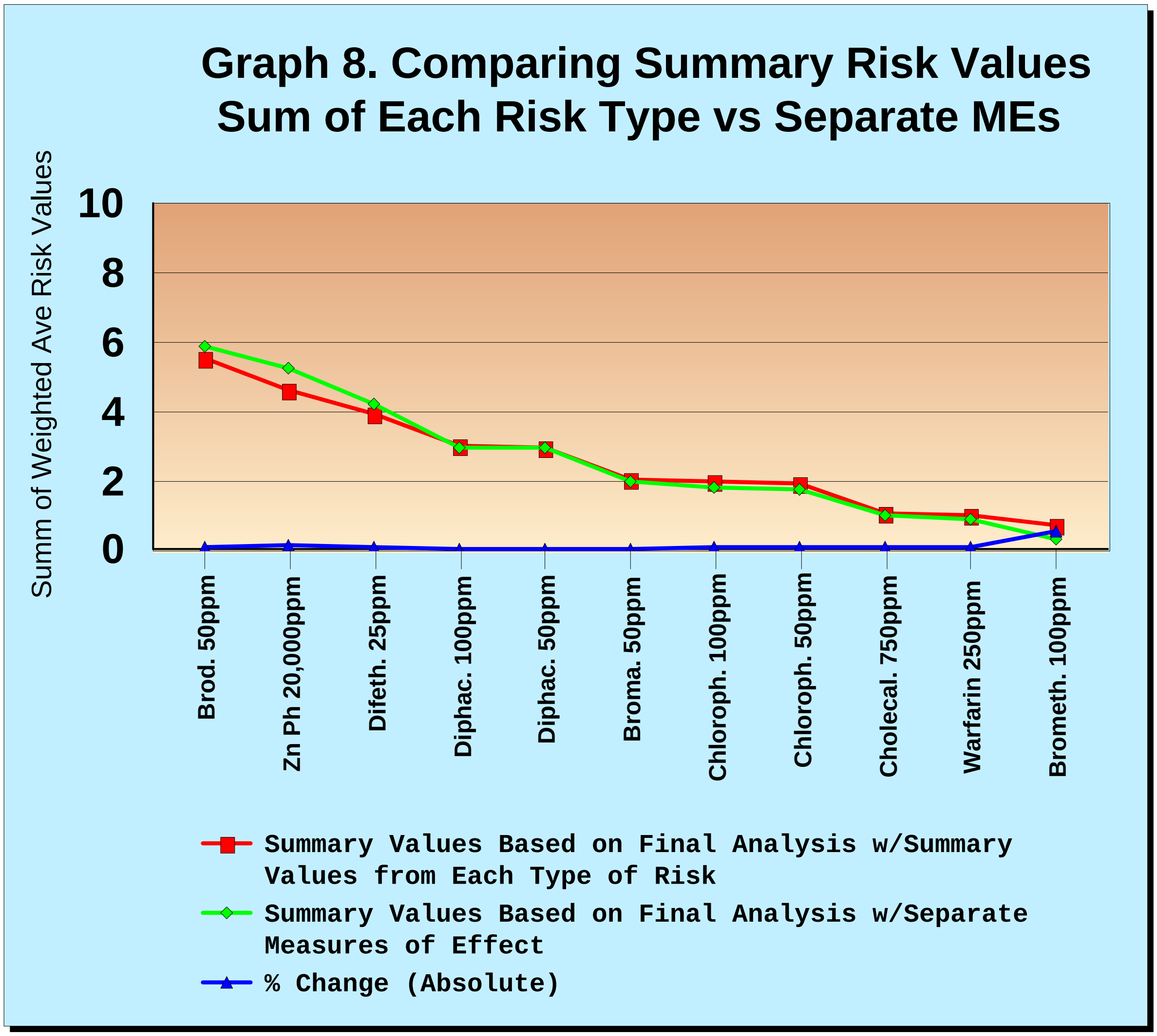
Rodenticide	mg ai/kg bait	Primary risks		Secondary risks		Summary values
		birds	mammals	birds	mammals	
Brodifacoum	50	5.58	1.25	8.60	6.76	5.55
Bromadiolone	50	0.10	0.71	3.03	4.40	2.06
Bromethalin	100	0.10	0.10	2.20	0.44	0.71
Chlorophacinone	100	0.14	0.16	0.03	7.62	1.99
Chlorophacinone	50	0.07	0.08	0.03	7.62	1.95
Cholecalciferol	750	0.12	0.18	2.00	2.00	1.07
Difethialone	25	4.15	0.45	6.29	4.82	3.93
Diphacinone	100	0.01	0.43	3.18	8.42	3.01
Diphacinone	50	0.01	0.22	3.18	8.42	2.96
Warfarin	250	0.04	0.83	1.72	1.32	0.98
Zinc Phosphide	20,000	7.81	10.00	0.00	0.69	4.63

Figure 6. Comparative Analysis Model Summary Values For Overall Risks to Birds and Nontarget Mammals



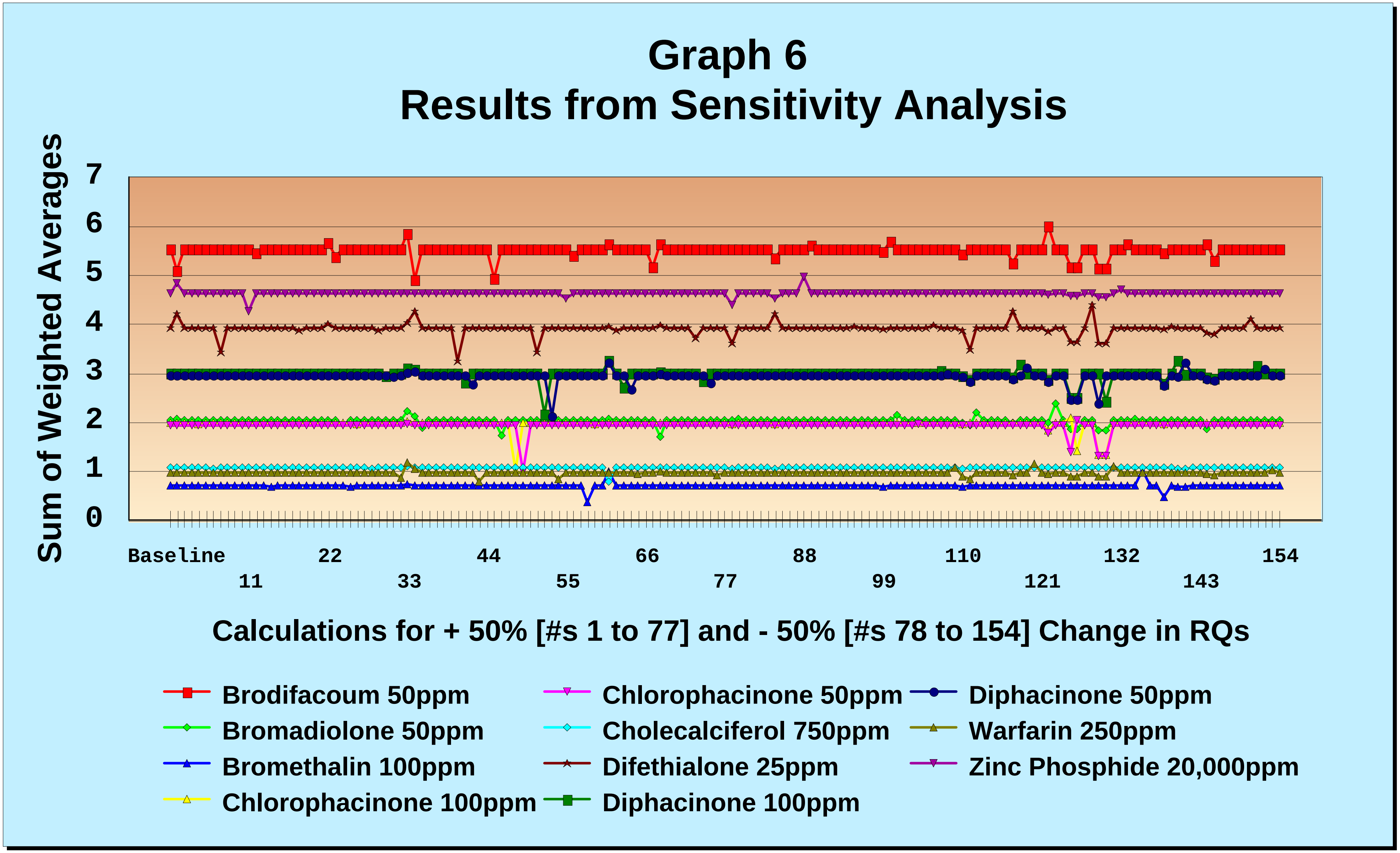
The approach taken for the overall analysis is to analyze each risk type separately, then analyze the summary values for each of the four risk types together. Each type of risk included variable and unequal numbers of measures of effect. Analyzing them separately and using summary values to derive an overall risk value eliminates unequal weighting of one risk over another due to differences in the number of measures of effect. An alternate approach is to consider all measures of effect in a single step and ignore unequal weighting. This alternate approach did not result in a change in the rankings (see Fig. 6).

Figure 7. Comparative Analysis Model Results Summary Values For Overall Risks When All Measures of Effect Are Considered in One Step



The sensitivity analysis (Fig. 7) indicates that the comparative analysis model rankings are robust, especially for brodifacoum, zinc phosphide and difethialone. Their ranking as the three rodenticides posing the greatest overall potential risk do not change when values for the measures of effect are varied by ±50%. See Appendix C for additional details of the sensitivity analysis.

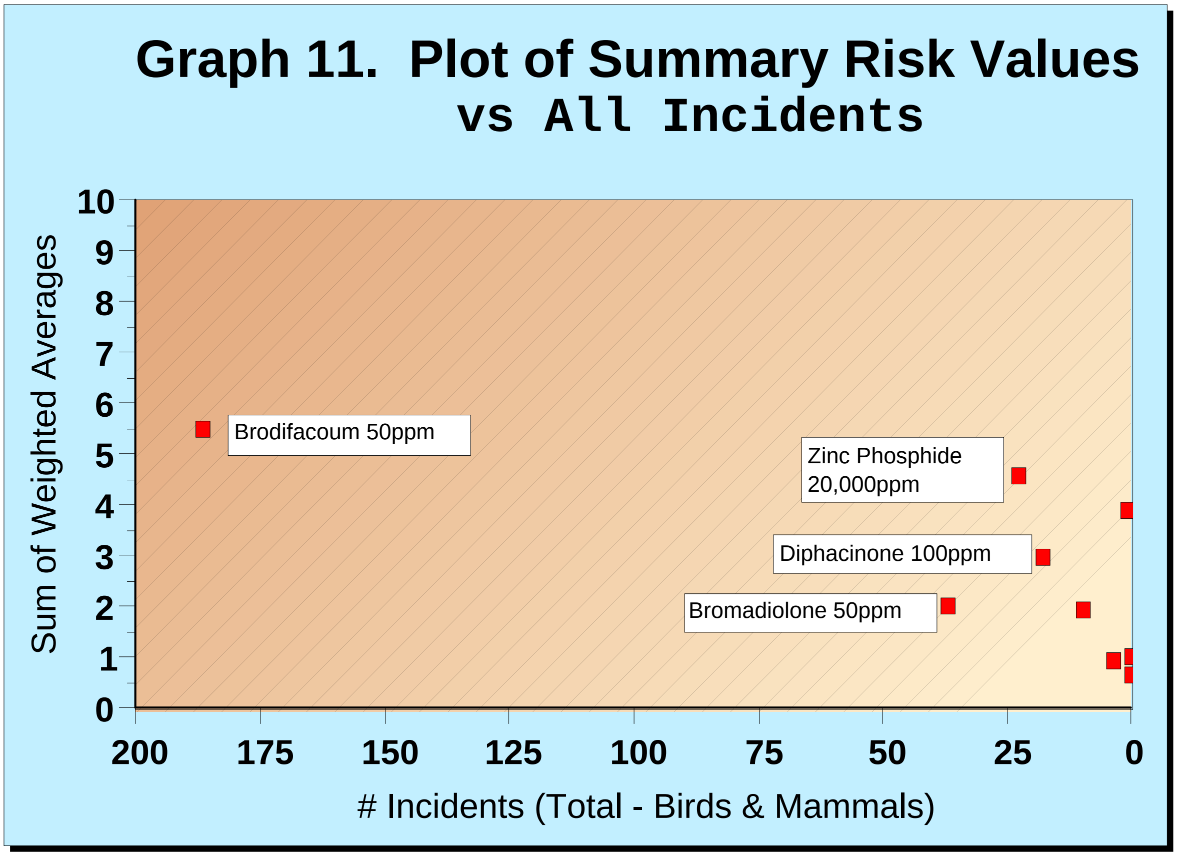
Figure 8. Sensitivity Analysis of Measure-of-effect Values Used in the Comparative Analysis Model. Each measure-of-effect value is separately decreased by 50% and then increased by 50%.



Lack of data for some rodenticides accounts for the most uncertainty in the comparative analysis model results. Data gaps include no secondary-hazards data for difethialone and few for bromethalin and cholecalciferol. For difethialone, which is highly similar to brodifacoum but used at a lower ai in baits (50 ppm vs 25 ppm), an assumption is made that secondary mortality would be about 80% of that reported for brodifacoum. Data are sufficient to distinguish differences in potential primary risks between 50 ppm and 100 ppm chlorophacinone and diphacinone baits but are insufficient to assess differences in secondary risks. Also, few if any data are available regarding retention time in blood and/or liver for some rodenticides, especially first-generation anticoagulants and the non-anticoagulants.

The incident data are not included in the comparative analysis model results but are meaningful for characterizing risk. A comparison of incidents versus the summary risk values for each rodenticide bait is depicted in Figure 9 (see graphs 9 and 10 in Attachment C for separate plots for birds and mammals). The baits with the most incidents and highest risk values are in the upper left, whereas those with the fewest incidents and lowest risk values are in the lower right portion of the graph. Brodifacoum is distinguished by its high summary value and high number of incidents in relation to the other rodenticides. Distinctions cannot be made between the 50 ppm and 100 ppm chlorophacinone and diphacinone baits in the incident data, but the 100 ppm baits are likely to present greater risk than the 50 ppm baits.

Figure 9. Plot of Summary Risk Values Versus Number of Incidents For Each Rodenticide



A “lines-of-evidence” assessment was performed based on the available data and supporting information. Each rodenticide is assigned a rating of high, moderate, or low for primary risk to birds, primary risk to nontarget mammals, secondary risk to birds, and secondary risk to mammals (Table 49). Differences among the rodenticides in their potential primary and secondary risks to birds are pronounced. Brodifacoum, and possibly difethialone, baits present the highest potential overall primary and secondary risks to birds and nontarget mammals. Brodifacoum is hazardous to birds and mammals, is persistent, and is widely used for commensal rodent control (see Table 2 for over-the-counter sales in 1996 and 1997). Difethialone is also hazardous to birds and mammals and it is very similar to brodifacoum (e.g., chemical structure, acute-toxicity profile). However, some uncertainty exists when comparing difethialone risks to brodifacoum risks, because market-share and use information and secondary-hazards data are lacking.

Based on the lines-of-evidence assessment, potential primary risks to birds are highest for zinc phosphide, brodifacoum, and difethialone. A small bird finding and eating a pellet or two of any of these baits is likely to ingest a lethal dose, and just a few pellets could provide a lethal dose to larger birds. In contrast, it seems highly unlikely that any small bird could eat 100 to 1000 pellets in a single feeding, which would be needed to provide an LD50 dose from a first-generation anticoagulant, bromadiolone, or cholecalciferol bait. Avian dietary RQs for zinc phosphide, brodifacoum, and difethialone greatly exceed the Agency’s LOC for acute risk to birds, whereas they are not or only slightly exceeded for other rodenticides. The dietary RQ provides some useful information for comparing potential risks among rodenticide baits but is based on birds feeding continuously on rodenticide bait for several days. Although some birds might do so, others might only find one or a few pellets in a foraging bout. Therefore, the number of pellets needed to be eaten to provide an LD50 dose may be a more appropriate approximation of potential risk than is the dietary RQ. Nevertheless, the characterization of risk does not change based on the method used to estimate potential risk.

Brodifacoum and difethialone clearly present a greater potential risk to raptors and avian scavengers than do the other rodenticides. Risks posed by brodifacoum are apparent from experimental and other control applications in outdoor settings and from many incidents involving owls, hawks, eagles, corvids and other birds. Concern about risks of second-generation anticoagulants to avian predators and scavengers is widely expressed in the rodenticide literature (Colvin et al. 1988; Hegdal and Colvin 1988; Joermann 1998; Howald et al. 1999; Stephenson et al. 1999; Stone et al. 1999), and the need to monitor residues and population trends is evident (Newton et al. 1990, 1999). This need is especially critical for brodifacoum, because it is so widely used for commensal-rodent control and because it may pose a greater potential risk compared to the other rodenticides.

Rodenticide baits are not selective to the target species. Some baits pose a greater hazard than others, but all rodenticides pose a risk to small nontarget mammals that eat bait, and many pose a potential risk to mammals that prey or scavenge dead or dying rodents that have eaten bait. Baits are formulated to be lethal to small mammals, and many small nontarget mammals are likely to find and eat bait available around the outside of buildings, inside barns and farm or utility shed, or in other outdoor settings.

Table 49. Primary and Secondary Risk Presumptions For Birds and Nontarget Mammals

Rodenticide	Primary risks		Secondary risks	
	birds	mammals	birds	mammals
Second-generation anticoagulants				
Brodifacoum	high	high	high	high
Difethialone	high	high	high	high
Bromadiolone	low to moderate	high	moderate	high
First-generation anticoagulants				
Diphacinone	low	high	moderate	high
Chlorophacinone	low to moderate	high	low	high
Warfarin	low	high	low	moderate
Others (non-anticoagulants)				
Bromethalin	moderate to high	high	insufficient data available	
Zinc phosphide	high	high	low	low
Cholecalciferol	low to moderate	high	insufficient data available	

The anticoagulants present a potential secondary risk to mammals, although warfarin probably to a lesser extent than the others. The incident data in Attachment D helps characterize and corroborate these risks. Zinc phosphide potentially poses minimal risks to either predatory birds or mammals, but insufficient data are available for bromethalin and cholecalciferol.

Eason et al. (2001) assessed risks of brodifacoum to nontarget birds and mammals in New Zealand, where brodifacoum is widely used to control rodents and possums. They conclude that ". . . the recorded mortality of birds after some control operations, coupled with the detection of brodifacoum residues in a range of wildlife including native birds and feral game animals raises serious concerns about the long-term effects of the targeted field use of brodifacoum or its use around farms where wildlife might encounter poisoned carcasses." Eason et al. (in prep.) also note: "On an international level we note that the reports of non-target wildlife mortality and contamination in raptors and mustelids from anticoagulants are on the increase (Shore *et al.*, 1999; Howald *et al.* 1999; Stone *et al.* 1999; B. Hosea, pers. comm.) and we strongly recommend that residue-monitoring programmes are established in those countries where anticoagulants are used in the field or extensively around farm buildings. An improved understanding of the risk associated with this class of compound will be achieved when there is a better understanding of whether or not food-chain contamination is occurring. The development of 'biomarkers' of exposure for different bird species will assist those agencies involved in wildlife protection."

More information also is needed on the potential adverse sublethal effects of rodenticides. Newton et al. (1990) note that ". . . there remains the possibility that sub-lethal levels of rodenticide may predispose death from other causes, or reduce the chance of recovery from accidents." Eason and Murphy (2001) emphasize that the risk of brodifacoum is magnified by its persistence, which could lead to accumulation on repeated exposure. A compound that is rapidly metabolized or excreted from a primary consumer may result in a lesser risk than one that bioaccumulates with repeated sublethal exposure, even if repeated exposure occurs weeks or even months after the initial exposure. Those compounds more rapidly cleared from the body are less likely to pose such long-term risk. Unfortunately, most laboratory tests and risk assessments do not consider the potential for bioaccumulation of the highly persistent anticoagulant compounds. Sublethal effects on reproduction will be considered when the data become available.

Uncertainty and Data Needs

A number of factors contribute uncertainty to the assessment. Those that appear to contribute the greatest uncertainty are: (1) missing data, including acute, chronic, and secondary toxicity as well as retention of some active ingredients in the liver, blood, and other body tissues; (2) the variable quality and quantity of existing data on metabolism and retention times in rodents and nontarget species; (3) specific use information by formulation, including typical amounts applied by use site, seasonally, and annually; distances applied from buildings; amounts used in rural versus urban areas; use by Certified Applicators versus homeowners and other non-certified applicators; and other such relevant information; (4) information on the number and species of birds and nontarget mammals frequenting baited areas and their likelihood of their finding and consuming bait or poisoned primary consumers in the various use areas; (5) methods to determine liver concentration(s) and total body burdens of rodenticide that would corroborate death or even if such a cause-effect relationship is appropriate (e.g., the "threshold of toxicity" concentration); (6) not accounting for the impacts of sublethal effects on reproduction and nontarget mortality (e.g., clotting abnormalities, hemorrhaging, stress factors including environmental stressors, such as adverse weather conditions, food shortages, and predation); (7) not accounting for bioaccumulation of repeated sublethal exposures to bait or poisoned rodents utilized as food by predators and scavengers; and (8) lack of incident reporting.

The greatest reduction in uncertainty for these analyses is likely to come from addressing data gaps where data is missing or needs to be standardized because quality is variable, as well as obtaining specific use and exposure information. Some of the concerns about adverse sublethal effects can be addressed through reproduction studies, which the Agency will require for all pesticides with outdoor uses. The no-observable-adverse-effects concentration (NOAEC) established from these studies will be a more appropriate indicator of a toxicity threshold than is the liver residue in dead animals.

Endangered Species Considerations

In response to a formal consultation requested by EPA (1991b) under Section 7 of the Endangered Species Act, the United States Fish and Wildlife Service issued a Biological Opinion on *Effects of 16 Vertebrate Control Agents On Threatened and Endangered Species* in March, 1993 (USFWS 1993). The Biological Opinion included jeopardy determinations for mammals, birds, and reptiles potentially exposed via primary or secondary exposure to brodifacoum, bromadiolone, chlorophacinone, diphacinone, warfarin, bromethalin, zinc phosphide, and cholecalciferol. For each species addressed in the Biological Opinion, the Service determined either that use of the rodenticide "is likely to jeopardize" or "is not likely to jeopardize" the continued existence of the species. For the likely-to-jeopardize determinations the Service provided "reasonable and prudent alternatives" that preclude jeopardy but still allow use of the rodenticide. These alternatives represent the Service’s best professional judgement of the measures necessary to provide the appropriate level of protection to the species. The Service also provided "incidental take" statements and "reasonable and prudent measures" to minimize take. Table 50 indicates the number of species, by rodenticide, for which the Service made a likely-to-jeopardize determination. The species addressed, jeopardy and no-jeopardy determinations, and the Service’s reasonable and prudent alternatives and/or measures are tabulated for each of the 8 rodenticides in Attachment E. Difethialone, first registered in 1995, is not addressed in this or any subsequent Biological Opinion, but EPA believes the jeopardy determinations for brodifacoum also would be applicable for difethialone.

Table 50. USFWS (1993) Jeopardy Determinations For Endangered and Threatened Species at Risk From Use of Each Rodenticide (Except Difethialone).

Rodenticide	no. species likely at jeopardy		
	mammals	birds	reptiles
Brodifacoum	10	2	0
Bromadiolone	7	0	0
Chlorophacinone	20	1	0
Diphacinone	28	1	0
Warfarin	10	0	0
Bromethalin	10	0	0
Zinc phosphide	16	9	0
Cholecalciferol	10	0	0
Total no. species	29	11	0

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Literature Cited

Ahmed, M.S., J. Baroch, L. Carlet, and D. Whaley. 1996. Secondary hazard study using chlorophacinone-killed laboratory rats fed to domestic ferrets (*Mustela putorius furo*). Unpubl. report submitted to EPA by LiphaTech, Inc., Milwaukee, WI. 84 pp.

Aiello, S.E., ed. 1998. The Merck Veterinary Manual (8th edition). Merck and Co., Whitehouse Station, NJ. Pages 2072-2073.

Alterio, N. 1996. Secondary poisoning of stoats (*Mustela erminea*), feral ferrets (*Mustela furo*), and feral house cats (*Felis catus*) by the anticoagulant poison, brodifacoum. New Zealand J. Zool. 23:331-338.

Alterio, N., K. Brown, and H. Moller. 1997. Secondary poisoning of mustelids in a New Zealand *Nothofagus* forest. J. Zool., London 243:863-869.

Anonymous. 1978. Unpubl. report, *Forschungsstelle für Jagdkunde und Wildschadenverhütung*. Bonn (DE) (in German).

Anonymous. 1980. [Study on the secondary hazard to birds by poisoned mice]. Boehringer Ingelheim, unpublished report.

Anonymous. 1981. Environmental and vertebrate chemistry - rodenticides. Agricultural Science Service, Research and Development Report, pp. 36-38.

Anonymous. 1983. Unpubl. Report Niedersächsische Forstliche Versuchsanstalt, Göttingen (DE) (in German).

Anonymous. 2001. Analysis of the supporting data for EPA's EIIS database with respect to rodenticides. Unpubl. report prepared for the Rodenticide Registrants Task Forceto EPA by Arcadis Geraghty and Miller, Millersville, MD. 29 pp.

Askham, L. 1988. Chlorophacinone - secondary hazard evaluation of chlorophacinone in raptors. Unpubl. report submitted to EPA by Lipha Chemicals, Inc., Milwaukee, WI. 30 pp.

Askham, L.R. and R.M. Poché. 1992. Biodeterioration of chlorophacinone in voles, hawks and an owl. Mammalia 56:145-150.

Aulerich, R.J., R.K. Ringer, and J. Safronoff. 1987. Primary and secondary toxicity of warfarin, sodium monofluoroacetate, and methyl parathion in mink. Arch. Environ. Contam. Toxicol. 16:357-366.

Bachmann, K.A. and T.J. Sullivan. 1983. Dispositional and pharmacodynamic characteristics of brodifacoum in warfarin-sensitive rats. Pharmacol. 27: 281–288.

Bachhuber, E. and C. Beck. 1988. [The effect of some anticoagulants on mice relevant in forestry and on mice predators.] Thesis, Munchen (DE) (in German).

Bai, K.M. and M.K. Krishnakumari. 1986. Acute oral toxicity of warfarin to poultry, *Gallus domesticus*: a non-target species. Bull. Environ. Toxicol. 37:544-549.

Back, N., R. Steger, and J.M. Glassman. 1978. Comparative acute oral toxicity of sodium warfarin and microcrystalline warfarin in the Sprague-Dawley rat. Pharmacol. Research Comm. 10:445-452.

Baril, S. and G. Pallister. 1981. Laboratory determinations of acute oral LD50 and efficacy of brodifacoum on the Richardson ground squirrel *Spermophilus richardsonii*. Montana Dept. Agric., Environ. Manage. Div. Technical Report 81-1. 13 pp.

Baroch, J. 1994a. Field efficacy of rodent bait diphacinone treated grains (0.01% SLN No. CA 890022 and 0.005% SLN No. CA 890020) using spot-baiting applications to control the California ground squirrel (*Spermophilus beecheyi*). Unpubl. report submitted to EPA by the California Department of Food and Agriculture, Sacramento.

Baroch, J. 1994b. Field efficacy of rodent bait diphacinone treated grain (0.005% SLN No. CA 890020) used in bait stations to control the California ground squirrel (*Spermophilus beecheyi*). Unpubl. report submitted to EPA by the California Department of Food and Agriculture, Sacramento.

Baroch, J. 1996a. Field efficacy of rodent bait chlorophacinone treated grains (0.01% SLN No. CA 890024 and 0.005% SLN No. CA 890023) using spot-baiting applications to control the California ground squirrel (*Spermophilus beecheyi*). Unpubl. report submitted to EPA by the California Department of Food and Agriculture, Sacramento. 87 pp.

Baroch, J. 1996b. Field efficacy of rodent bait chlorophacinone treated grain (0.005% SLN No. CA 890023) used in bait stations to control the California ground squirrel (*Spermophilus beecheyi*). Unpubl. report submitted to EPA by the California Department of Food and Agriculture, Sacramento. 79 pp.

Baroch, J. 1997. Secondary hazard study using chlorophacinone-killed laboratory rats fed to black-billed magpies (*Pica pica*). Unpubl. report submitted to EPA by LiphaTech, Inc., Milwaukee, WI. 77 pp.

Batten, P. and H. Bratt. 1990. Brodifacoum: elimination from the tissues of rats following administration of single oral doses. Unpubl. report submitted to EPA by ICI Americas, Inc., Wilmington, DE. 65 pp.

Bell, H.B. and R.W. Dimmick. 1975. Hazards to predators feeding on prairie voles killed with zinc phosphide. J. Wildl. Manage. 39:816-819.

Belleville, M.J. 1981. Absorption, distribution, metabolism and excretion studies in the rat using ^{14}C-labeled chlorophacinone. Unpubl. report submitted to EPA by Lipha Chemicals, Inc., New York. 14 pp.

Belleville, M. 1986. Toxi-kinetics and metabolism: 1. study performed with the molecule marked ^{14}C; 2. study performed with the cold molecule. Unpubl. report submitted to EPA by LiphaTech, Inc., Milwaukee, WI. 133 pp.

Belleville, M. 1991. Compared hepatic kinetics of brodifacoum and difethialone in the rat, after oral administration of 0.06 mg/kg once weekly for 4 consecutive weeks. Unpubl. report submitted to EPA by LiphaTech, Inc., Milwaukee, WI. 39 pp.

Berny, P.J., T. Buronfosse, F. Buronfosse, F. Lamarque, and G. Lorgue. 1997. Field evidence of secondary poisoning of foxes (*Vulpes vulpes*) and buzzards (*Buteo buteo*) by bromadiolone, a 4-year survey. Chemosphere 35:1817-1829.

Borst, G.H.A. and G.H.M. Counotte. 2000. Shortfalls using second-generation anticoagulant rodenticides. J. Zoo and Wildl. Med. 33:85.

Bratt, H. and P. Hudson. 1979. Brodifacoum: absorption, excretion and tissue retention in the rat. Unpubl. report submitted to EPA by ICI Americas, Inc. 30 pp.

Breckenridge, A.M., S. Cholerton, J.A.D. Hart, B.K. Park, and A.K. Scott. 1985. A study of the relationship between the pharmacokinetics and pharmacodynamics of 4-hydroxycoumarin anticoagulants, warfarin, difenacoum, and brodifacoum in the rabbit. British J. Pharmacol. 84: 81–91.

Brown, P., A. Charlton, M. Cuthbert, L. Barnett, L. Ross, M. Green, L. Gillies, K. Shaw, and M. Fletcher. 1996. Identification of pesticide poisoning in wildlife. J. Chromatography A 754:463-478.

Buckle, A.P. 1994. Rodent control methods: chemical. Pages 127-160 in A.P. Buckle and R.H. Smith (eds), Rodent Pests and Their Control. CAB International, London.

Bullard, R.W., R.D. Thompson, and G. Holgvin. 1976: Diphenadione (diphacinone) residue in tissue of cattle. J. Agric. Food Chem. 24:261–263.

Byers, R.E. 1978. Performance of rodenticides for the control of pine voles in orchards. J. Amer. Soc. Hort. Sci. 103:65-69.

California Department of Pesticide Regulation. (undated). Applicator training materials for endangered species identification.
www.cdpr.ca.gov/docs/es/espdfs/baitsta1.pdf
www.cdpr.ca.gov/docs/es/espdfs/baitsta2.pdf

Carlet, L. and J.J. Mach 1997. Secondary hazard study using warfarin-killed black-tailed prairie dogs (*Cynomys ludovicianus*) fed to domestic ferrets (*Mustela putorius furo*). Unpubl. report submitted to EPA by Genesis Laboratories, Inc., Wellington, CO. 18 pp.

CDFG. 1962. Economic poisons (pesticides) investigations. California Dept. Fish and Game, Wildlife Laboratory, Pittman-Robinson Wildlife Restoration Proj. W-52-B-6. 10 p.

Christopher, M.J., M. Balasubramanyam, and K.R. Purushotham. 1984. Toxicity of three anticoagulant rodenticides to male hybrid leghorns. Zool. 71:275-281.

Clark, J.P. 1994. Vertebrate Pest Control Handbook. (4th ed.) California Dept. Food and Agriculture, Sacramento. 803 pp.

Colvin, B.A., P.L. Hegdal, and W.B. Jackson. 1988. Review of non-target hazards associated with rodenticide use in the USA. Bull. OEPP/EPPO Bull. 18:301-308.

Colvin, B.A., W.B. Jackson, and P.L. Hegdal. 1991. Secondary poisoning hazards associated with rodenticide use. Pages 60-64 in E.D. Magallona (ed.), Proc. 11th Int. Cong. Plant Protection, Vol. I, October 5-9, 1987, Manila, Philippines.

Cox , P. and R.H. Smith. 1992. Rodenticide ecotoxicology: pre-lethal effects of anticoagulants on rat behavior. Proc. Vertebr. Pest Conf. 15:165-170.

Crabtree, D.G. and W.H. Robison. 1952. Warfarin and its effect on some wildlife species. Trans N. Amer. Wildl. Conf. 17:167-173.

Delley, B. and E. Joseph. 1985. Prévention des pullulations de Campagnols terrestres en prairie de montagne - acquis récents et perspetives de développement d'appâts rodenticides. Schweiz. Landw. Forsch 24:121-178.

Diaz, L.I. and D.M. Whitacre. 1976. Excretion and retention of ^{14}C-diphacinone in rats. Unpubl. report, submitted by Velsicol Chemical Corporation. 8 pp.

Doty, R.E. 1945. Rat control on Hawaiian sugarcane plantations. Hawaiian Planters Record 49:71-239.

Dowding, J.E., E.C. Murphy, and C.R. Veitch. 1999. Brodifacoum residues in target and non-target species following an aerial poisoning operation on Motuihe Island, Hauraki Gulf, New Zealand. New Zealand J. Ecol. 23:207-214.

Dubock, A.C. and D.E. Kaukeinen. 1978. Brodifacoum (Talon™ rodenticide), a novel concept. Proc. Vertebr. Pest Conf. 8:127-137.

Duckett, J.E. 1984. Barn owls (*Tyto alba*) and the second generation rat-baits utilised in oil palm plantations in Peninsular Malaysia. Planter, Kualar Lumpur 60:3-11.

Eason, C.T. and E.B. Spurr. 1995. Review of the toxicity and impacts of brodifacoum on non-target wildlife in New Zealand. New Zealand J. Zool. 22:371-379.

Eason, C.T. and E. Murphy. 2001. Recognising and reducing secondary and tertiary risks associated with brodifacoum. Pages 157-163 in J. J. Johnston (ed.), Pesticides and Wildlife. American Chemical Society Symposium Series 771.

Eason, C.T., G.R. Wright, and D. Batcheler. 1996. Anticoagulant effects and the persistence of brodifacoum in possums (*Trichosurus vulpecula*). New Zealand J. Agric. Research 39:397-400.

Eason, C.T., G.R. Wright, L. Meikle, and P. Elder. 1996. The persistence and secondary poisoning risks of sodium monofluoroacetate (1080), brodifacoum, and cholecalciferol in possums. Proc. Vertebr. Pest Conf. 17:54-58.

Eason, C.T., M. Wickstrom, P. Turck, and G.R.G Wright. 1999. A review of recent regulatory and environmental toxicology studies on 1080: results and implications. New Zealand J. Ecol. 23:129–137.

Eason C., E. Murphy, G. Wright, C. O'Connor, and A. Buckle. (2001). Risk assessment of broad-scale toxicant application for rodent eradication on islands versus mainland use. In H-J. Pelz, D.P. Cowan and C.J. Feare (eds), Advances In Vertebrate Pest Management II, Filander Verlag, Furth. pp. 45-58.

ECOFRAM. 1999. Ecological Committee on FIFRA Risk Assessment Methods. Terrestrial Draft Report, May 10. 677 pp.

Edwards, P.J., R.A. Brown, and J.M. Coulson. 1988. Field methods for studying the non-target hazard of rodenticides. BCPC Monograph No. 40, Environmental Effects of Pesticides, pp. 77-88.

Empson, R.A. and C.M. Miskelly. 1999: The risks, costs and benefits of using brodifacoum to eradicate rats from Kapiti Island, New Zealand. New Zealand J. Ecol. 23: 241–254.

EPA. 1981. Warfarin and its Sodium Salt (3-(alpha-Acetonylbenzyl)-4-hydroxcoumarin). Pesticide Registration Standard. OPP/EPA. 131 pp.

EPA. 1982. Variation in toxicity of warfarin to rats. Unpubl. report, EPA Terrestrial and Aquatic Biology Unit, Beltsville, MD. 80 pp.

EPA. 1991a. Warfarin and its Sodium Salt. Reregistration Eligibility Document. SRRD/OPP/EPA. http://www.epa.gov/pesticides/reregistration/status.htm

EPA. 1991b. Formal request for Endangered Species Act Section 7 consultation on 31 pesticides for all uses, on all listed species. USEPA Office of Pesticides and Toxic Substances, Washington D.C. 290 pp.

EPA. 1992. Comparative analysis of acute avian risk from granular pesticides. Office of Pesticide Programs, USEPA, Washington, D.C. 71 pp.

EPA. 1993. Wildlife Exposure Factors Handbook (vol. I and II). EPA/600/R-93/187b. http://www.epa.gov/ncea/pdfs/introduc.pdf

EPA. 1994. Pesticide Regulation (PR) Notice 94-7: Label Improvement Program for the Revision of Use Directions for Commensal Rodenticides and Statement of the Agency's Policies on the Use of Rodenticide Bait Stations. www.epa.gov/opppmsd1/PR_Notices/pr94-7.html

EPA. 1998a. Reregistration Eligibility Decision (RED): Rodenticide Cluster. EPA738-R-98-007. 307 pp. http://www.epa.gov/pesticides/reregistration/status.htm

EPA. 1998b. Zinc Phosphide Reregistration Eligibility Decision (RED). EPA 738-R-98-006. http://www.epa.gov/pesticides/reregistration/status.htm

EPA. 1998c. Guidelines for Ecological Risk Assessment. EPA/630/R-95/002F, April 1998, Final. 171 pp. http://www.epa.gov/ncea/ecorsk.htm

EPA. 1998d. A Comparative Analysis of Ecological Risks from Pesticides and Their Use: Background, Methodology, Case Study http://www.epa.gov/scipoly/sap/1998/index.htm#december8

Erickson, W.A., R.E. Marsh, and W.L. Halvorson. 1990. A roof rat bait station that excludes deer mice. Wildl. Soc. Bull. 18:319-325.

Evans, J. 1965. Evaluations of zinc phosphide on nutria. Unpubl. report, Denver Wildlife Research Center. 31 pp.

Evans, J. and A.L. Ward. 1967. Secondary poisoning associated with anticoagulant-killed nutria. JAVMA 151:856-861.

Evans, J., J.O. Ellis, and R.E. Griffith, Jr. 1966. Results of testing zinc phosphide on Louisiana muskrats. Unpubl. report, Denver Wildlife Center. 12 pp.

Fagerstone, K.A. and P.L. Hegdal. 1998. Risk assessment of rodenticides through use of telemetry and other methods: 5 examples. Pages 49-66 in L.W. Brewer and K.A. Fagerstone (eds), Radiotelemetry Applications for Wildlife Toxicology Studies. SETAC Press.

Fisher, D.D. and R.M. Timm. 1987. Laboratory trial of chlorophacinone as a prairie dog toxicant. Proc. Great Plains Wildl. Damage Workshop 8:67-69.

Fletcher, J.S., J.E. Nellessen, and T.G. Pfleeger. 1994. Literature review and evaluation of the EPA food-chain (Kenaga) nomogram, an instrument for estimating pesticide residues on plants. Environ. Tox. Chem. 13:1383-1391.

Ford, M. 1993. Rodenticides. Pages 322-327 in P. Viccellio (ed.), Handbook of Medical Toxicology. Little, Brown, and Co., Boston.

Gaines, T.B. 1969. Acute toxicity of pesticides. Toxicol. Applied Pharmacol. 14:515-534.

Glahn, J.F. and L.D. Lamper. 1983. Hazards to geese from exposure to zinc phosphide rodenticide baits. Calif. Fish and Game 69:105-114.

Godfrey, M.E.R. 1985. Non-target and secondary poisoning hazards of "second generation" anticoagulants. Acta Zoologica Fennica 173:209-212.

Godfrey, M.E.R. 1986. An evaluation of the acute-oral toxicity of brodifacoum to birds. Proc. Vertebr. Pest Conf. 12:78-81.

Godfrey, M.E.R., T.C. Reid, and H.J.F. McAllum. 1981. The acute toxicity of the anticoagulant brodifacoum to dogs. N. Z. J. Experimental Agric. 9:147-149.

Goldade, D.A., P.J. Savarie, J.C. Hurley, S.A. Gaddis, and J.J. Johnson. 2001. Design of a laboratory secondary hazard study. Pages 146-156 in J. J. Johnston (ed.), Pesticides and Wildlife. American Chemical Society Symposium Series 771.

Goodall, M.J., T.M. Primus, and J.J. Johnston. 2002. Determination of chlorophacinone and diphacinone residues in California ground squirrels and non-target animals. Unpubl. report QA 976, National Wildlife Research Center, Fort Collins, CO, submitted to EPA by the California Department of Food and Agriculture, Sacramento. 119 pp.

Goodwin, P. and G. Wright. 1998. Decision analysis for management judgement, 2nd ed. John Wiley & Sons, England. 454 pp.

Gray, A., C.V. Eadsforth, A.J. Dutton, and J.A. Vaughan. 1994. Toxicity of three second generation rodenticides to barn owls. Pestic. Sci. 42:179-184.

Grolleau, G., G. Lorgue, and K. Nahas. 1989. Toxicitd secondaire, en laboratoire, d'un rodenticide anticoagulant (bromadiolone) pour des pr6dateurs de rongeurs champétres: buse variable (*Buteo buteo*) et hermine (*Mustela erminea*). Bull. OEPP/EPPO Bull. 19:633-648.

Gunther, R., L.J. Felice, R.K. Nelson, and A.M. Franson. 1988. Toxicity of vitamin D_3 rodenticide to dogs. JAVMA 193:211-214.

Hagan, E.C. and J.L. Radomski. 1953. The toxicity of 3-(acetonylbenzyl)-4-hydroxycoumarin (warfarin) to laboratory animals. J. Amer. Pharm. Assoc. 42:379-382.

Harling, R., P. Buford, and S. Freyer. 1986. LM2219 (difethialone) oral toxicity study in beagle dogs (13 weeks). Unpubl. report, Huntingdon Research Centre, UK.

Hawkins, D.R., R.R. Brodie, D. Clarke, and C. Brindley. 1991. Determination of the residues and half-life of the rodenticides brodifacoum, bromadiolone, and flocoumafen in the livers of rats during 200 days after a single oral dose of each at a dose level of 0.2 mg/kg. Unpubl. report submitted to EPA by LiphaTech, Inc. Milwaukee, WI. 78 pages.

Hegdal, P.L. 1985. Primary hazards to game birds associated with the use of ramik brown (diphacinone bait) for controlling voles in orchards. Unpubl. study, Denver Wildlife Research Center. 53 pp.

Hegdal, P.L. and T.A. Gatz. 1977. Hazards to pheasants and cottontail rabbits associated with zinc phosphide baiting for microtine rodents in orchards. Unpubl. report, Denver Wildlife Research Center. 60 pp.

Hegdal, P.L. and R. W. Blaskiewicz. 1984. Evaluation of the potential hazard to barn owls of talon (brodifacoum bait) used to control rats and house mice. Environ. Toxicol. Chem. 3:167-179.

Hegdal, P.L. and B.A. Colvin. 1988. Potential hazard to eastern screech-owls and other raptors of brodifacoum bait used for vole control in orchards. Environ. Toxicol. Chem. 7:245-260.

Hill, E.F. and J.W. Carpenter. 1982. Responses of siberian ferrets to secondary zinc phosphide poisoning. J. Wildl. Manage. 46:678-685.

Hilton, H.W., L.F. Pank, and A.H. Teshima. 1972. Progress report on two years of rat control with zinc phosphide bait. Unpubl. report (Tech. Suppl. to Ins. Rat Control Rep. 24), Hawaiian Sugar Planters Association, Hilo. 20 pp.

Hoerger, F., and E.E. Kenaga. 1972. Pesticide residues on plants: correlation of representative data as a basis for estimation of their magnitude in the environment. In F. Coulston and F. Korte, eds., Environmental Quality and Safety: Chemistry, Toxicology, and Technology, Georg Thieme Publ, Stuttgart, West Germany, pp. 9-28.

Hone, J. and H. Mulligan. 1982. Vertebrate pesticides. Science Bull. 89, Dept. of Agriculture, NSW, Australia. 130 pp.

Hosea, R.C. 2000. Exposure of non-target wildlife to anticoagulant rodenticides in California. Proc. Vertebr. Pest Conf. 19:236-244.

Hosea, R.C., B.J. Finlayson, and E.E. Littrell. 2001. Forensic investigative techniques to identify impacts (primary and secondary) from three groups of pesticides on raptors in California. Pages 38-51 in J. J. Johnston (ed.), Pesticides and Wildlife. American Chemical Society Symposium Series 771.

Howald, G. 1997. The risk of non-target species poisoning from brodifacoum used to eradicate rats from Langara Island, British Columbia, Canada. MS Thesis, Univ. British Columbia, Vancouver, BC. 159 pp.

Howald, G.R., P. Mineau, J.E. Elliott, and K.M. Cheng. 1999. Brodifacoum poisoning of avian scavengers during rat control on a seabird colony. Ecotoxicol. 8:431-447.

Howald, G.R., B.R. Tershy, B.S. Keitt, H. Gellerman, S. Ortega, K. Faulkner, C. J. Donlan, and D.A. Croll. 2001. Progress in rat eradication, Anacapa Island, Channel Islands National Park, California. Unpubl. report submitted to EPA by the National Park Service, USDI. 17 pp.

Hygnstrom, S.E., R.M. Timm, and G.E. Larson. 1994. Prevention and Control of Wildlife Damage. Univ. Nebraska Cooperative Extension, USDA Animal Damage Control, and Great Plains Agric. Council.

ICI Americas, Inc. 1978a. Talon™: secondary toxicity of brodifacoum to foxes. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 13 pp.

ICI Americas, Inc. 1978b. Talon™: secondary toxicity of brodifacoum to dogs (beagles). Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC.

ICI Americas, Inc. 1979a. Forty-day LC50 - laughing gull. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 12 pp.

ICI Americas, Inc. 1979b. Forty-day dietary LC50 - laughing gull. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 17 pp.

ICI Americas, Inc. 1979c. Brodifacoum residues in rodents, pheasants and ground rat tissues. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 29 pp.

ICI Americas, Inc. 1981. VOLAK: potential hazard of the 50 ppm black pellet broadcast at three rates as indicated by penned ring-necked pheasants (Virginia). Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC.

ICI Americas, Inc. 1983. Brodifacoum residues in screech owls and other wildlife from VOLID-treated apple orchards. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 40 pp.

Jackson, W.B. and A.D. Ashton. 1992. A review of available anticoagulants and their use in the United States. Proc. Vertebr. Pest Conf. 15:156-160.

Jackson, W.B., S.R. Spaulding, R.B.L. van Lier, and B.A. Dreikorn. 1982. Bromethalin - a promising new rodenticide. Proc. Vertebr. Pest Conf. 10:10-16.

Janda, J. and M. Bosseova. 1970. The toxic effect of zinc phosphide baits on partridges and pheasants. J. Wildl. Manage. 34:220-223.

Jaques, L.B. 1959. Dicoumarol drugs and the problem of haemorrhage. J. Canad. Med. Assoc. 81:848-854.

Jobsen, J.A. 1978. [Study on the possibility of secondary poisoning of ferrets by chlorophacinone-poisoned muskrats.] Internal report of the Dutch Plant Protection Service, Wageningen (NL).

Joermann, G. 1998. A review of secondary poisoning studies with rodenticides. Bull. OEPP/EPPO Bull. 28:157-176.

Johnson, G.D. and K.A. Fagerstone. 1994. Primary and secondary hazards of zinc phosphide to nontarget wildlife - a review of the literature. USDA/APHIS/DWRC Research Report No. 11-55-005. 26 pp.

Jones, F.J.S. and M.G. Townsend. 1978. Warfarin: *in vivo* studies on Japanese quail. Pages 219-220 in Pest Infestation Control Lab. Rep. 1974-76. HMSO, London.

Kamil, N. 1987. Kinetics of bromodialone, anticoagulant rodenticide, in the Norway rat (*Rattus norvegicus*). Pharmacol. Res. Communications 19:767–775.

Kaukeinen, D.E. 1982. A review of the secondary poisoning hazard potential to wildlife from the use of anticoagulant rodenticides. Proc. Vertebr. Pest Conf. 10:151-158.

Kaukeinen, D.E. 1993. Nontarget organism evaluations for rodenticides. Pages 352-363 in K.D. Racke and A.R. Leslie (eds), Pesticides in Urban Environments: Fate and Significance. ACS Symposium Series, American Chemical Society, Washington, DC.

Kaukeinen, D.E., C.W. Spraggins, and J.F. Hobson. 2000. Risk-benefit considerations in evaluating commensal anticoagulant rodenticide impacts to wildlife. Proc. Vertebr. Pest Conf. 19:245-256.

Kosmin, M. and J.N. Barlow. 1976. Rodent control using a novel formulation of diphacinone, Ramik. Proc. 1st Afro-Asian Vertebr. Pest Congr., Nov. 8-11, 1976. Cairo, Egypt.

Laas, F.J., D.A. Forss, and M.E.R. Godfrey. 1985. Retention of brodifacoum in sheep tissues and excretion in faeces. New Zealand J. Agric. Research 28:357-359.

Labe, J. and G. Lorgue. 1977. Intoxication des carnivores domestiques par les raticides anticoagulants. pp128-140. Notes de Toxicologie Veterinaire, No. 3. Centre d'Informations Toxicologiques Veterinaire, Ecole Nationale Veterinaire, Marcy L'Etoile, France.

LaVoie, G.K. 1990. A study of the toxicity of the anticoagulant brodifacourn to American kestrels (*Falco sparverius*). Proc. Third International Conference on Plant Protection in the Tropics, IV, pp. 27-29.

Lechevin, J.C. and R.M. Poché. 1988. Activity of LM 2219 (difethialone), a new anticoagulant rodenticide, in commensal rodents. Proc. Vert. Pest Conf. 13:59-63.

Lee, C.H. 1994. Secondary toxicity of some rodenticides to barn owls. 4th International Conf. Plant Protection in the Tropics, 28-31 March, Kuala Lumpur, Malaysia, pp. 161-163.

LiphaTech, Inc. 1997. The veterinarian’s guide to managing poisoning by anticoagulant rodenticides. Brochure available from Liphatech, Inc., 3600 West Elm Street, Milwaukee, WI. 16 pp.

Lisella, F.S., K.R. Long, and H.G. Scott. 1971. Toxicology of rodenticides and their relationship to human health. Part II, J. Environ. Health 33:361-365.

Lorgue, G. 1986. Acute oral toxicity study of LM2219 (difethialone) in cats. Unpubl. report, Ectoxicology Laboratory (INRA-ENVL), National Veterinary School, Lyon, France.

Lund, M. 1981. Hens, eggs and anticoagulants. Int. Pest Control 5:127-128.

Lund, M. and A.M. Rasmussen. 1986. Secondary poisoning hazards to stone martens (*Martes foina*) fed bromadiolone-poisoned mice. Nordic Veterinary-Medicine 38:241-243.

Lutz, W. 1986. [Study on the possible secondary-poisoning hazard to buzzards (*Buteo buteo*) by the rodenticide bromadiolone.] Unpubl. Report for BBA, Forschungsstelle für Jagdkunde und Wildschadenverhütung. Bonn (DE) (in German).

Lutz, W. 1987. [Study on the possible secondory poisoning hazard to buzzards (*Buteo buteo* L.) by the rodenticide brodifacoum]. Forschungsstelleftir Jagdkunde und Wildschadenverhiitung. Unpubl. report for BBA.

Mach, J.J. 1998. Secondary hazard study using warfarin-killed prairie dogs (*Cynomys ludovicianus*) fed to domestic ferrets (*Mustela putorius furo*). Unpubl. report submitted to EPA by Genesis Laboratories, Inc., Wellington, CO. 64 pp.

Mach, J.J. and K.L. March. 1997. Secondary hazard study using warfarin-killed laboratory rats fed to black-billed magpies (*Pica pica*). Unpubl. report submitted to EPA by Genesis Laboratories, Inc., Wellington, CO. 21 pp.

Machlin, L.J. 1984. Handbook of vitamins: nutritional, biochemical, and clinical aspects. Marcel Dekker, Inc., New York. 464 pp.

Mackintosh, C.G., F.J. Laas, M.E.R. Godfrey, and K. Turner. 1988. Vitamin K_1 treatment of brodifacoum poisoning in dogs. Proc. Vertebr. Pest Conf. 13:86-90.

Marsh, R.E. 1985. Are anticoagulant rodenticides a problem for household pets? Pest Control 53(8):20-22,24 and 53(9):26-28,31.

Marsh, R.E. and W.E. Howard. 1978. Secondary toxicity hazards tests of brodifacoum to raptors. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 17 pp.

Marsh, R.E. and W.E. Howard. 1986. Ground squirrel--coyote secondary toxicity studies with chlorophacinone and bromadiolone (an administrative report of laboratory findings). Unpubl. report submitted to EPA by LiphaTech, Inc., Milwaukee, WI.

Marsh, R.E. and A.E. Koehler. 1991. Potential secondary hazards of cholecalciferol. Unpubl. report submitted to EPA by Bell Laboratories, Inc., Madison, WI.

Marsh, R.E., W.E. Howard, and W.B. Jackson. 1980. Bromadiolone: a new toxicant for rodent control. Pest Control, August.

Marshall, E.F. 1984. Cholecalciferol: a unique toxicant for rodent control. Proc. Vertebr. Pest Conf. 11:95-98.

Massey, G., L. Valutis, and J. Marzluff. 1997. Secondary poisoning effects of diphacinone on Hawaiian crows: a study using American crows as surrogates. Unpubl. report, U. S. Fish and Wildlife Service, Pacific Islands Office. 12 pp.

Mastrota, F.N. 1999. Wildlife mortality incidents caused by pesticides: an analysis of the EIIS database. Poster presented at The Wildlife Society 6th Annual Conference, September 7-11, Austin, Texas.

Matschke, G.H. and G.K. LaVoie. 1976. Zinc phosphide - a literature review. Unpubl. report, Denver Wildlife Research Center. 45 pp.

Matschke, G.H., K.A. Fagerstone, S.F. Baril, and R.W. Blaskiewicz. 1983. Population reduction of Richardson's ground squirrels using a brodifacoum bait. Proc. Great Plains Wildl. Damage Control Workshop 6:34-44.

Matschke, G.H. and K.J. Andrews. 1990. Zinc phosphide: black-tailed prairie dog - domestic ferret secondary poisoning study. Unpubl. report, Denver Wildlife Research Center. 80 pp.

McCann, J.A., W. Teeters, D.J. Urban and N. Cook. 1981. A short-term dietary toxicity test on small mammals. Pages 132-142 in D.W. Lamb and E.E. Kenaga (eds): Avian and Mammalian Wildlife Toxicology: Second Conference, ASTM STP 757, American Society for Testing Materials.

McDonald, R.A., S. Harris, G. Turnbull, P. Brown, and M. Fletcher. 1998. Anticoagulant rodenticides in stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) in England. Environ. Pollution 103:17-23.

Meehan, A.P. 1984. Rats and mice: their biology and control. Rentokil Limited, East Grinstead, Great Britain.

Meenken, D., K. Wright, and A. Couchman. 1999. Brodifacoum residues in possums (*Trichosurus vulpecula*) after baiting with brodifacoum cereal bait. New Zealand J. Ecol. 23:215-217.

Mendenhall, V.M. and L.F. Pank. 1980. Secondary poisoning of owls by anticoagulant rodenticides. Wildl. Soc. Bull. 8:311-315.

Merson, M.H., R.E. Byers, and D.E. Kaukeinen. 1984. Residues of the rodenticide brodifacoum in voles and raptors after orchard treatment. J. Wildl. Manage. 48:212-216.

Michigan Wildlife Diseases Manual. (undated). Zinc phosphide. www.dnr.state.mi.us/wildlife/division/RoseLake

Mineau, P. A. Baril, B.T. Collins, J. Duffe, G. Joermann, and R. Littik. 2001. Pesticide acute toxicity reference values. Rev. Environ. Contam. Toxicol. 170:13-74.

Morgan, D.R., G.R. Wright, S.C. Ogilvie, R. Pierce, and P. Thomson. 1996. Assessment of the environmental impact of brodifacoum during rodent eradication operations in New Zealand. Proc. Vertebr. Pest Conf. 17:213–218.

Mount, M.E. and B.F. Feldman. 1983. Mechanism of diphacinone rodenticide toxicosis in the dog and its therapeutic implications. Amer. J. Veterinary Res. 44:2009-2017.

Munday, J.S. and L.J. Thompson. 2003. Brodifacoum toxicosis in two neonatal puppies. Vet. Pathol. 40:216-219.

Murphy, E.C., B.K. Clapperton, P.M.F. Bradfield, and H.J. Speed. 1998. Brodifacoum residues in target and non-target animals following large-scale poison operations in New Zealand podocarp-hardwood forests. New Zealand J. Zool. 25:307-314.

Nagy, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57:111-128.

Nelson, P.C. and G.J. Hickling. 1994. Pindone for rabbit control: efficacy, residue, and costs. Proc. Vertebr. Pest Conf. 16:217-222.

Newton, I., I. Wyllie, and P. Freestone. 1990. Rodenticides in British barn owls. Environmental Pollution 68:101-117.

Newton, I., R.F. Shore, I. Wyllie, J.D.S. Birks, and L. Dale. 1999. Empirical evidence of side-effects of rodenticides on some predatory birds and mammals. Pages 347-367 in D.P. Cowan and C.J. Feare (eds), Advances in Vertebrate Pest Management. Filander Verlag, Fürth.

O'Brien, P.H., J.A. Beck, and B.S. Lukins. 1987. Residue tissue levels of warfarin and 1080 in poisoned feral pigs. Unpublished report presented at the Australian Vertebrate Pest Control Conference.

O'Reilly, R.A., P.M Aggeler,.and L.S. Leong. 1963. Studies on the coumarin anticoagulant drugs: the pharmacodynamics of warfarin in man. J. Clinical Investigations 4:5142–1551.

Ogilvie, S.C., R.J. Pierce, G.R.G. Wright, L.H. Booth, and C.T. Eason. 1997. Brodifacoum residue analysis in water, soil, invertebrates, and birds after rat eradication on Lady Alice Island. New Zealand J. Ecol. 21:195-197.

Palmer, V.A. 1999. Brodifacoum rodenticides. Memorandum to E. Dassatti, Chief, Bureau of Pesticide Management, NY State Dept. Environmental Conservation, May 11, 1999.

Pank, L.F. 1972. Secondary hazards. Unpubl. report, Denver Wildlife Research Center. 2 pp.

Pank, L.F. and D.N. Hirata. 1976. Primary and secondary toxicity of anticoagulant rodenticides. Unpubl. report, Denver Wildlife Research Center. 23 pp.

Pank, L.F., J.K. Crier, R.D. Nass, D.N. Hirata, and R.S. Stott. 1972. Mammal damage control research–Hawaiian agricultural crops. Unpubl. report (pp. 6-10 in annual progress report), Denver Wildlife Research Center.

Papworth, D.S. 1958. A review of the dangers of warfarin poisoning to animals other than rodents. J. Royal Soc. Health 78:52-60.

Parmar, G., H. Bratt, R. Moore, and P.L. Batten. 1987. Evidence for a common binding site *in vivo* for the retention of anticoagulants in rat liver. Human Toxicol. 6:431–432.

Pelfrene, A.F. 1991. Synthetic organic rodenticides. Handbook of Pesticide Toxicology, vol. 3: Classes of Pesticides, pages 1271-1316. Academic Press, Inc.

Poché, R.M. 1986. The status of bromadiolone in the United States. Proc. Vertebr. Pest Conf. 12:6-15.

Poché, R.M. 1988. Rodent tissue residue and secondary hazard studies with bromadiolone. Bull. OEPP/EPPO Bull. 18:323-330.

Poché, R.M. and J.J. Mach. 2001. Wildlife primary and secondary toxicity studies with warfarin. Pages 181-196 in J. J. Johnston (ed.), Pesticides and Wildlife. American Chemical Society Symposium Series 771.

Prier, M.S. and P.H. Derse. 1962. Evaluation of the hazard of secondary poisoning by warfarin-poisoned rodents. JAVMA 140:351-354.

Primus, T.M., J.D. Eisemann, G.H. Matschke, C. Ramey, and J.J. Johnson. 2001. Chlorophacinone residues in rangeland rodents: an assessment of the potential risk of secondary toxicity to scavengers. Pages 164-180 in J. J. Johnston (ed.), Pesticides and Wildlife. American Chemical Society Symposium Series 771.

Pyrola, K. 1968. Sex differences in the clotting factor response to warfarin and of warfarin metabolism in the rat. Annales Medicinal Experimentalis et Biologiae Fennicae 46:23–34.

Quy, R.J., D.P. Cowan, C.V. Prescott, J.E. Gill, G.M. Kerins, G. Dunsford, A. Jones, and A.D. MacNicoll. 1995. Control of a population of Norway rats resistant to anticoagulant rodenticides. Pestic. Sci. 45:247-256.

Radvanyi, A., P. Weaver, C. Massari, D. Bird, and E. Broughton. 1988. Effects of chlorophacinone on captive kestrels. Bull. Environ. Contam. Toxicol. 41:441-448.

Ramey, C.A., R.T. Sterner, J.O. Wolff, and W.D. Edge. 1994. Observed nontarget hazards to ring-necked pheasants and California quail of broadcasting a 2% zinc phosphide oat groats bait for control of gray-tailed voles in alfalfa. Unpubl. report, QA-332, Denver Wildlife Research Center. 515 pp.

Ramey, C.A. J.B. Bourassa, J.E. Brooks, K.A. Fagerstone, and M. Furuta. 1998. Non-target hazard to free-ranging ring-necked pheasants exposed to 2% zinc phosphide grain bait broadcast for vole control in alfalfa. Unpubl. report, QA-408, National Wildlife Research Center, Fort Collins, CO. 199 pp.

Riedel, M., Riedel, B., and H. Schlegelmilch. 1991. [Risk of secondary intoxication for birds of prey and owls following use of chlorophacinone baits against common voles.] Unpubl. Report (in German).

Ringer, R. and R. Aulerich. 1978. Determination of oral LD50 of brodifacoum for mink. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 19 pp.

Robben, J.H., E.A. Kujpers, and H.C. Mout. 1998. Plasma superwarfarin levels and vitamin K_1 treatment in dogs with anticoagulant rodenticide poisoning. Veterin. Quart. 20:24–27.

Robertson, H.A., R.M. Colbourne, P.J. Graham, P.J. Miller, and R.J. Pierce. 1999. Survival of brown kiwi (*Apteryx mantelli*) exposed to brodifacoum poison in Northland, New Zealand. New Zealand J. Ecol. 23:225-231.

Ross, D.B., N.L. Roberts, and C.N.K. Phillips. 1979a. Assessment of the palatability of "Talon" pellets containing 0.005% (50 ppm) brodifacoum to the bobwhite quail. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 16 pp.

Ross, D.B., N.L. Roberts, and C.N.K. Phillips. 1979b. Assessment of the palatability of "Talon" pellets containing 0.005% (50 ppm) brodifacoum to the ring-necked pheasant. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 16 pp.

Rymph, B. (ed.). 1994. Assessing Pesticide Impacts on Birds: Final Report of the Avian Effects Dialogue Group, 1988-1993. RESOLVE Center for Environmental Dispute Resolution, Washington, DC. 156 pp.

Salmon, T.P., D.A. Whissom, and W.P. Gorenzel. 2002. Field efficacy studies comparing 0.005% and 0.01% diphacinone and chlorophacinone baits for controlling California ground squirrels (*Spermophilus beecheyi*). Unpubl. report submitted to EPA by the California Department of Food and Agriculture, Sacramento. 131 pp.

Saucy, F., A. Meylan, and R. Poitry. 2001. Lessons from 18 years of use of anticoagulants against fossorial *Arvicola terrestris* in Switzerland. In J. Pelz, P. D. Cowan, and C. J. Feare (eds), Advances in Vertebrate Pest Management, Vol. 2, Filander Verlag. Fürth, pp. 71-90.

Savarie, P.J. 1991. The nature, modes of actions, and toxicity of rodenticides. Pages 589-598 in D. Pimentel (ed.), CRC Handbook of Pest Management in Agriculture (Vol. II).

Savarie, P.J. and R.K. LaVoie. 1979. Secondary toxicity hazards of the anticoagulant brodifacoum to American kestrels (*Falco sparverius*). Unpubl. report, Denver Wildlife Research Center. 24 pp.

Savarie, P.J. and E.W. Schafer, Jr. 1986. Biodeterioration of warfarin, sodium monofluoroacetate, 4-aminopyridine and 3-chloro-4-methylbenzenamine in terrestrial vertebrate pests. Pages 66-73 in S. Barry and D.R. Houghton (eds), Biodeterioration 6, Proc. 6th International Biodeterioration Symp., Washington, D.C., August 1984. CAB International, London.

Savarie, P.J., D.J. Hayes, R.T. McBride, and J.D. Roberts. 1979. Efficacy and safety of diphacinone as a predacide. Pages 69-79 in E.E. Kenaga (ed.), Avian and Mammalian Wildlife Toxicology, ASTM STP 693, American Society for Testing and Materials.

Schafer, E.W., Jr. and W.A. Bowles, Jr. 1985. Acute oral toxicity and relellency of 933 chemicals to house and deer mice. Arch. Environ. Contam. Toxicol. 14:111-129.

Schafer, E.W., Jr., J. Guarino, and R. Brunton. 1970. Effects of zinc phosphide on blackbirds. Unpubl. report, Denver Wildlife Research Center. Unpubl. report submitted to EPA by ICI Americas, Inc., Goldsboro, NC. 3 pp.

Schitoskey Jr., F. 1975. Primary and secondary hazards of three rodenticides to kit fox. J. Wildl. Manage. 39:416-418.

Shore, R.F., J.D.S. Birks, and P. Freestone. 1999. Exposure of non-target vertebrates to second-generation rodenticides in Britain, with particular reference to the polecat *Mustela putorius*). New Zealand J. Ecol. 23:199-206.

Shore, R.F., J.D.S. Birks, P. Freestone, and A.C. Kitchener. 1996. Second-generation rodenticides and polecats (*Mustela putorius*) in Britain. Environ. Pollution 91:279-282.

Siegfried, W.R. 1968. The reactions of certain birds to rodent baits treated with zinc phosphide. Ostrich 39:197-198.

Spaulding, S.R. and H. Spannring. 1988. Status of bromethalin outside the United States. Proc. Vertebr. Pest Conf. 13:64-69.

Stephenson, B.M., E.O. Minot, and D.P. Armstrong. 1999. Fate of moreporks (*Ninox novaeseelandiae*) during a pest control operation on Mokoia Island, Lake Rotorua, North Island, New Zealand. New Zealand J. Ecol. 23:233-240.

Sterner, R.T. 1996. Zinc phosphide residues in voles: scenarios showing low risks to domestic cats and dogs. Vertebr. Pest Conf. 17:139-142.

Sterner, R.T. and R.E. Mauldin. 1995. Regressors of whole-carcass zinc phosphide/phosphine residues in voles: indirect evidence of low hazards to predators/scavengers. Arch. Environ. Contam. Toxicol. 28:519-523.

Sterner, R.T., D.A. Goldade, and R.E. Mauldin. 1998. Zinc phosphide residues in gray-tailed voles (*Microtus canicaudus*) fed fixed particles of a 2% grain bait. Internat. Biodeter. Biodegradation 42:109-113.

Sterner, W. 1978. [Study on secondary-poisoning hazards of the rodenticide chlorophacinone in the system mouse-carrion crow.] International Bio-Research, Walsrode. Unpubl. Report to BBA (DE).

Sterner, W. 1981. [Study on secondary-poisoning hazards of Lepit-Feldmausköder to white storks.] International Bio-Research, Walsrode. Unpubl. Report to Schering AG.

Stone, W.B., J.C. Okonlewski, and J.R. Stedelin. 1999. Poisoning of wildlife with anticoagulant rodenticides in New York. J. Wildl. Diseases 35:187-193.

Stone, W.B., J.C. Okonlewski, and J.R. Stedelin. 2003. Anticoagulant rodenticides and raptors: recent findings from New York, 1998-2001. Bull. Environ. Contam. Toxicol. 70:34-40.

Taylor, D.P. 1984. The identification and detection of the rats in New Zealand and the eradication of ship rats on Tawhitiwini Island. Unpubl. dissertation, Lincoln College, Canterbury, New Zealand.

Telle, H.-J. 1955. [The use of cumarin-containing products in rodent control]. Nachrichtenblatt des deutschen Pflanzenschutzdienstes 4:93-99.

Thijssen, H.H.W. 1995. Warfarin-based rodenticides: mode of action and mechanism of resistance. Pest. Sci. 43:73-78.

Thorsen, M., R. Shorten, R. Lucking, and V. Lucking. 2000. Norway rats (*Rattus norvegicus*) on Frégate Island, Seychelles: the invasion; subsequent eradication attempts and implications for the island's fauna. Biol. Conservation 96:133-138.

Tietjen, H.P. 1976. Zinc phosphide–its development as a control agent for black-tailed prairie dogs. Spec. Sci. Rep.--Wildl. No. 195, USFWS, Washington, DC. Unpubl. report, Denver Wildlife Research Center. 14 pp.

Til, H.P., M.T. Spanjers, and E.J. Sinkeldam. 1974. Acute and subacute oral toxicity studies with pyrancumarin and warfarin in cats, hens and quail. Unpubl. report, submitted to EPA by Prentiss Drug and Chemical Co., Inc., New York.

Timm, R.M. 1994. Norway rats. Pages B-105 to B-120 in S.E. Hygnstrom, R.M. Timm, and G.E. Larson (eds), Prevention and Control of Wildlife Damage. Univ. Nebraska Cooperative Extension, USDA Animal Damage Control, and Great Plains Agric. Council.

Tkadlec, W. and B. Rychnovsky. 1990. Residues of Zn_3P_2 in the common vole (*Microtus arvalis*) and secondary poisoning hazards to predators. Folia Zoologica 39:147-156.

Towns, D., I. McFadden, and T. Lovegrove. 1993. Offshore islands co-operative conservation project with ICI Crop Care Division: phase one (Stanley Island). Science and Research Internal Report No. 138, New Zealand Dept. Conservation, Wellington.

Towns, D., I. McFadden, P. Thomson, H. Robertson, and R. Colbourne. 1994. Offshore islands co-operative conservation project with ICI Crop Care Division: phase two (Red Mercury Island). Wellington, Department of Conservation, Science and Research Internal Report No. 142, New Zealand Dept. Conservation, Wellington.

Townsend, M.G., M.R. Fletcher, E.M. Odam, and P.I. Stanley. 1981. An assessment of the secondary poisoning hazard of warfarin to tawny owls. J. Wildl. Manage. 45:242-248.

Townsend, M.G., P.J Bunyan, E.M Odam, P.I. Stanley, and H.P. Wardall. 1984. Assessment of secondary poisoning hazard of warfarin to least weasels. J. Wildl. Manage. 48:628-632.

USFWS. 1993. Biological Opinion: Effects of 16 Vertebrate Control Agents On Threatened and Endangered Species. March, 1993. Reprinted by EPA. 168 pp.

van Lier, R.B.L. 1981. A secondary toxicity study in beagle dogs maintained for two weeks on diets derived from bromethalin (EL-614, Compound 126814) treated rodents. Unpubl. report submitted to EPA by Eli Lilly Co.

Vyas, N.B. 1999. Factors influencing estimation of pesticide-related wildlife mortality. Toxicol. Industrial Health 15:186-191.

Walker, K. and G. Elliott. 1997. Effect of the poison brodifacoum on non-target birds on the Chetwode Islands. Ecol. Manage. 5:21-27.

Weitzel, J.N., J.A. Sadowski, B.C. Furie, R. Moroose, H. Kim, M.E. Mount, M.J. Murphy, and B. Furie. 1990. Surreptitious ingestion of a long-acting vitamin K antagonist/rodenticide, brodifacoum: clinical and metabolic studies of three cases. Blook 76:2555–2559.

WHO. 1995. Anticoagulant rodenticides. Environmental Health Criteria 175, International Programme on Chemical Safety. World Health Organization, Geneva.

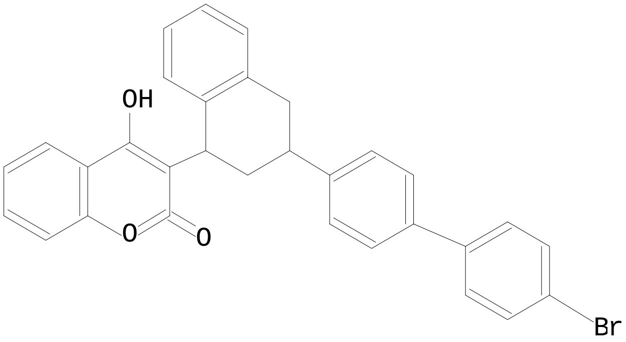
Woody, B.J., M.J. Murphy, A.C. Ray, and R.A. Green. 1992. Coagulopathic effects and therapy of brodifacoum toxicosis in dogs. J. Veterin. Internal Medicine 6:23–28.

Wyllie, I. 1995. Potential secondary poisoning of barn owls by rodenticides. Pesticide Outlook 6:19-25.

Yu, C.C., Y.H. Atallah, and D.M. Whitacre. 1982. Metabolism and disposition of diphacinone in rats and mice. Drug Metabolism and Disposition 10:645-648.

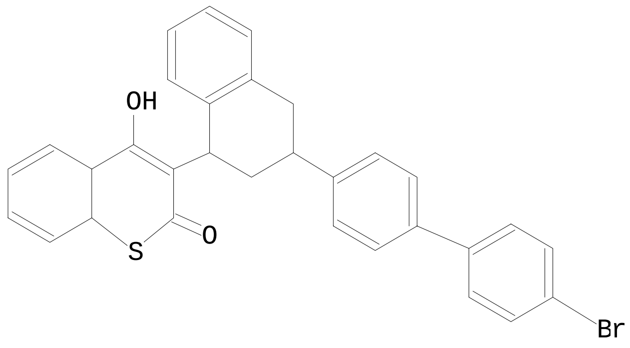
Attachment A: Chemical Structures and Selected Physical/Chemical Properties of the Rodenticides

Brodifacoum:

Chemical name:	3-[3-(4'-bromo[1,1'-biphenyl]-4-yl)-1,2,3,4-tetrahydro-1-naphthalenyl]-4-hydroxy-2H-1-benzopyran-2-one
Chemical structure:	
Class:	coumarin anticoagulant
Molecular formula:	$C_{31}H_{23}BrO_3$
Molecular weight:	523.4
Physical state:	solid
Melting point:	228-232º C
Solubility:	<10 ppm in water at 20º C, pH 7

Difethialone:

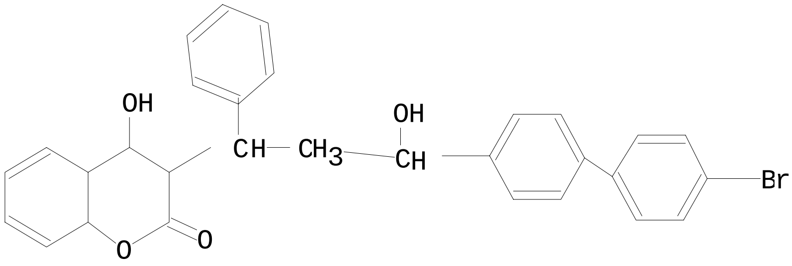
Chemical name:	3-[3-(4'-bromo[1,1'-biphenyl]-4-yl)-1,2,3,4-tetrahydro-1-naphthalenyl]-4-hydroxy-
Chemical structure:	



Class:	coumarin anticoagulant
Molecular formula:	$C_{31}H_{24}BrO_2S$
Molecular weight:	539.5
Physical state:	solid
Melting point:	230° C
Solubility:	0.39 ppm in water at 25° C

Bromadiolone:

Chemical name:	3-[3-(4'-bromo[1,1'-biphenyl]-3-hydroxy-1-phenylpropyl]-4-hydroxy-2H-1-benzopyrane-2-one
Chemical structure:	

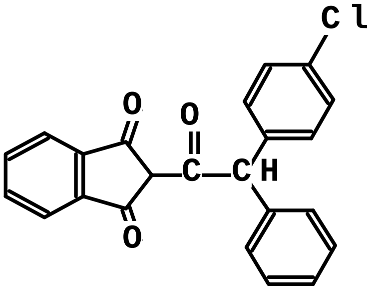


Class:	coumarin anticoagulant
Molecular formula:	$C_{30}H_{23}BrO_4$
Molecular weight:	527.4
Physical state:	solid
Melting point:	200-210° C
Solubility:	12 ppm in water at 20° C

Chlorophacinone:

Chemical name: 2-[(4-chlorophenyl)phenylacetyl]-1H-indene-1,3(2H)-dione

Chemical structure:



Class: indandione anticoagulant

Molecular formula: $C_{23}H_{14}O_3Cl$

Molecular weight: 373.8

Physical state: solid

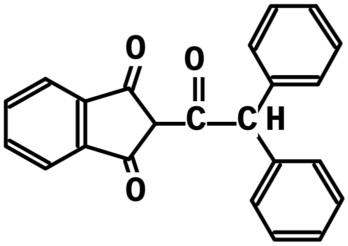
Melting point: 140° C

Solubility: 20-34 ppm

Diphacinone:

Chemical name: 2-(diphenylacetyl]-1H-indene-1,3(2H)-dione

Chemical structure:



Class: indandione anticoagulant

Molecular formula: $C_{23}H_{16}O_3$

Molecular weight: 340.4

Physical state: solid

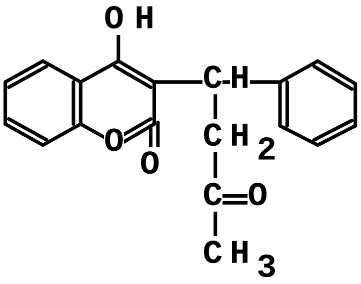
Melting point: 141-145^o C

Solubility: 17-30 ppm in water (not verified)

Warfarin:

Chemical name: 4-hydroxy-3-(3-oxo-1-phenylbutyl)-2H-1-benzopyran-2-one

Chemical structure:

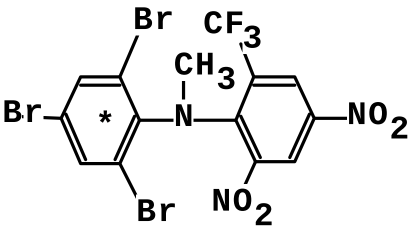


Class:	coumarin anticoagulant
Molecular formula:	$C_{19}H_{16}O_4$ $C_{19}H_{15}NaO_4$ (sodium salt)
Molecular weight:	308.4 330.1 (sodium salt)
Physical state:	solid
Melting point:	159-165^o C
Solubility:	0.196 ppm in water at 25^o C

Bromethalin:

Chemical name: N-methyl-2,4-dinitro-N-(2,4,6-tribromophenyl)-6-(trifluoromethyl)-benzenamine

Chemical structure:



Class: diphenylamine

Molecular formula: $C_{13}H_7Br_3F_3N_3O_4$

Molecular weight: 578.0

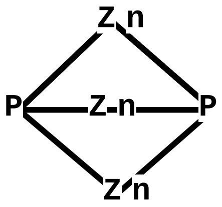
Physical state: solid

Melting point: 148-152°C

Solubility: 3.8 ppb at 25°C

Zinc phosphide:

Chemical name:	zinc phosphide
Chemical structure:	

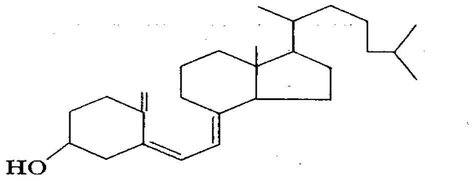


Class:	inorganic compound
Molecular formula:	Zn_3P_2
Molecular weight:	258.09
Physical state:	solid
Melting point:	420° C
Solubility:	reported to be insoluble in water

Cholecalciferol:

Chemical name: 9,10-Secocholesta-5,7,10(19)-trien-3 beta-ol

Chemical structure:



Class: sterol

Molecular formula: $C_{27}H_{44}O$

Molecular weight: 384.6

Physical state: solid

Melting point: 84-85° C

Solubility: no data available, but reported to be insoluble in water

Attachment B: Common and Scientific Names of the Birds and Mammals Cited in the Assessment

Order/ Common name	Scientific name	Family
Waterfowl (Anseriformes)		
Mallard	*Anas platyrhynchos*	Anatidae
Canada goose	*Branta canadensis*	Anatidae
White-fronted goose	*Anser albifrons*	Anatidae
Snow goose	*Chen caerulescens*	Anatidae
Paradise shelduck	*Tadorna variegata*	Anatidae
Grey duck	*Anas superciliosa*	Anatidae
Gallinaceous birds (Galliformes)		
Northern bobwhite	*Colinus virginianus*	Phasianidae
Ring-necked pheasant	*Phasianus colchicus*	Phasianidae
California quail	*Callipepla californica*	Phasianidae
Japanese quail	*Coturnix coturnix*	Phasianidae
Chukar	*Alectoris chukar*	Phasianidae
Gray partridge	*Perdix perdix*	Phasianidae
Turkey (wild)	*Meleagris gallopavo*	Phasianidae
Owls (Strigiformes)		
Barn owl	*Tyto alba*	Tytonidae
Great-horned owl	*Bubo virginianus*	Strigidae
Spotted eagle owl	*Bubo africanus*	Strigidae
Northern saw-whet owl	*Aegolius acadicus*	Strigidae
Eastern screech-owl	*Otus asio*	Strigidae
Long-eared owl	*Asio otus*	Strigidae
Short-eared owl	*Asio flammeus*	Strigidae
Spotted owl	*Strix occidentalis*	Strigidae
Tawny owl	*Strix aluco*	Strigidae
Barred owl	*Strix varia*	Strigidae
Snowy owl	*Nyctea scandiaca*	Strigidae
Morepork	*Ninox novaeseelandiae*	Strigidae

Order/ Common name	Scientific name	Family
Diurnal birds of prey (Falconiformes)		
Red-tailed hawk	*Buteo jamaicensis*	Accipitridae
Red-shouldered hawk	*Buteo lineatus*	Accipitridae
Eurasian buzzard	*Buteo buteo*	Accipitridae
Broad-winged hawk	*Buteo platypterus*	Accipitridae
Rough-legged hawk	*Buteo lagopus*	Accipitridae
Cooper's hawk	*Accipiter cooperii*	Accipitridae
Sharp-shinned hawk	*Accipiter striatus*	Accipitridae
Northern goshawk	*Accipiter gentilis*	Accipitridae
Golden eagle	*Aquila chrysactos*	Accipitridae
Bald eagle	*Haliaeetus leucocephalus*	Accipitridae
Eurasian harrier	*Circus pygargus*	Accipitridae
Australasian harrier	*Circus approximans*	Accipitridae
Kite	*Milvus migrans*	Accipitridae
American kestrel	*Falco sparverius*	Falconidae
Merlin	*Falso columbarius*	Falconidae
Peregrine falcon	*Falco peregrinus*	Falconidae
New Zealand falcon	*Falco novaeseelandiae*	Falconidae
Turkey vulture	*Cathartes aura*	Cathartidae
Black vulture	*Coragyps atratus*	Cathartidae
Herons (Ciconiformes)		
Great blue heron	*Ardea herodias*	Ardeidae
White stork	*Ciconia ciconia*	Ciconiidae
Gulls and shorebirds (Charadriiformes)		
Southern black-backed gull	*Larus dominicans*	Laridae
Laughing gull	*Larus atricilla*	Laridae
Black-billed gull	*Larus bulleri*	Laridae
Franklin's gull	*Larus pipixcan*	Laridae
Brown skua	*Catharacta skua*	Stercorariidae
New Zealand dotterel	*Charadrius obscurus*	Charadriidae
Variable oystercatcher	*Haematopus unicolor*	Haematopodidae

Order/ Common name	Scientific name	Family
Rails (Gruiformes)		
Weka	*Gallirallus australus*	Rallidae
Pukeko (purple gallinule)	*Porphyrio porphyrio*	Rallidae
Spotless crake	*Porzana tabuensis*	Rallidae
Parrots (Psittaciformes)		
Kaka	*Nestor meridionalis*	Psittacidae
Kakariki	*Cyanoramphus* sp.	Psittacidae
Pigeons/doves (Columbiformes)		
Mourning dove	*Zenaida macroura*	Columbidae
Kereru	*Hemiphaga novaeseelandiae*	Columbidae
Kiwi (Apterygiformes)		
Brown kiwi	*Apteryx mantelli*	Apterygidae
Perching Birds (Passeriformes)		
American crow	*Corvus brachyrhynchos*	Corvidae
Carrion crow	*Corvus corone*	Corvidae
Common raven	*Corvus corax*	Corvidae
Northwestern crow	*Corvus caurinus*	Corvidae
Fish crow	*Corvus ossifragus*	Corvidae
Black-billed magpie	*Pica pica*	Corvidae
Blue jay	*Cyanocitta cristata*	Corvidae
Australian magpie	*Gymnorhina tibicen*	Cracticidae
Myna	*Acridotheres tristis*	Sturnidae
House sparrow	*Passer domesticus*	Passeridae
Horned lark	*Eremophila alpestris*	Alaudidae
Lincoln’s sparrow	*Melospiza lincolnii*	Emberizidae
Song sparrow	*Melospiza melodia*	Emberizidae
Red-winged blackbird	*Agelaius phoeniceus*	Emberizidae
Canary	*Serinus canarius*	
Chaffinch	*Fringilla coelebs*	Fringillidae
Robin (New Zealand)	*Petroica australis*	Eopsalttriidae

Order/ Common name	Scientific name	Family
Tomtit	*Petroica macrocephala*	Eopsalttriidae
Fantail	*Rhipidura fuliginosa*	Monarchidae
Bellbird	*Anthornis melanura*	Meliphagide
Tui	*Prosthemadera novaeseelandiae*	Meliphagide
Saddleback	*Philesturnus carunculatus*	Callaeidae
Kokako	*Callaeas cinerea*	Callaeidae
Whitehead	*Mohoua ochrocephala*	Pachycephalidae
Silvereye	*Zosterops lateralis*	Zosteropidae
Blackbird (Eurasian)	*Turdus merula*	Muscicapidae
Rodents (Rodentia)		
Norway rat	*Rattus norvegicus*	Muridae
Roof rat (black rat, ship rat)	*Rattus rattus*	Muridae
Polynesian rat	*Rattus exulans*	Muridae
House mouse	*Mus musculus*	Muridae
Deer mouse	*Peromyscus maniculatus*	Muridae
Meadow vole	*Microtus pennsylvanicus*	Muridae
Pine vole	*Microtus pinetorum*	Muridae
Water vole	*Arvicola terrestris*	Muridae
Muskrat	*Ondatra zibethicus*	Muridae
Heermann’s kangaroo rat	*Dipodomys heermanni*	Heteromyidae
Banner-tailed kangaroo rat	*Dipodomys spectabilis*	Heteromyidae
San Joaquin pocket mouse	*Perognathus inornatus*	Heteromyidae
Botta’s pocket gopher	*Thomomys bottae*	Geomyidae
California ground squirrel	*Spermophilus beecheyi*	Sciuridae
Richardson’s ground squirrel	*Spermophilus richardsonii*	Sciuridae
Rock squirrel	*Spermophilus variegatus*	Sciuridae
Black-tailed prairie dog	*Cynomys ludovicianus*	Sciuridae
Gray squirrel	*Sciurus carolinensis*	Sciuridae
Fox squirrel	*Sciurus niger*	Sciuridae
Eastern chipmunk	*Tamias striatus*	Sciuridae

Order/ Common name	Scientific name	Family
Nutria (coypu)	*Myocastor coypus*	Myocastoridae
Insectivores (Insectivora)		
Dusky shrew (montane shrew)	*Sorex monticolus*	Soricidae
Rabbits/hares (Lagomorpha)		
Cottontail rabbit	*Sylvilagus floridanus*	Leporidae
Desert cottontail	*Sylvilagus auduboni*	Leporidae
Black-tailed jack rabbit	*Lepus californicus*	Leporidae
European rabbit	*Oryctolagus cuniculus*	Leporidae
European hare	*Lepus capensis*	Leporidae
Carnivores (Carnivora)		
Coyote	*Canis latrans*	Canidae
Red fox	*Vulpes vulpes*	Canidae
San Joaquin kit fox	*Vulpes macrotis mutica*	Canidae
Gray fox	*Urocyon cinereoargenteus*	Canidae
Mountain lion	*Felis concolor*	Felidae
Bobcat	*Lynx rufus*	Felidae
Lynx	*Lynx lynx*	Felidae
Badger	*Meles meles*	Mustelidae
Ermine (stoat)	*Mustela erminea*	Mustelidae
European ferret	*Mustela putorius furo*	Mustelidae
Siberian ferret	*Mustela eversmanni*	Mustelidae
Mink	*Mustela vison*	Mustelidae
Least weasel	*Mustela nivalis*	Mustelidae
Long-tailed weasel	*Mustela frenata*	Mustelidae
Polecat	*Mustela putorius*	Mustelidae
Striped skunk	*Mephitis mephitis*	Mustelidae
Stone marten	*Martes foina*	Mustelidae
Raccoon	*Procyon lotor*	Procyonidae
Mongoose	*Herpestes auropunctatus*	Herpestidae

Order/ Common name	Scientific name	Family
Marsupials (Marsupialia)		
Opossum	*Didelphis virginiana*	Didelphidae
Brushtail possum	*Trichosurus vulpecula*	Phalangeridae
Ungulates (Artiodactyla)		
White-tailed deer	*Odocoileus virginianus*	Cervidae
Roe deer	*Capreolus capreolus*	Cervidae
Boar (pig)	*Sus scrofa*	Suidae

Attachment C: Comparing Potential Risks of Rodenticide Baits to Birds and Mammals Using A Comparative Analysis Model

Prepared by: Douglas J. Urban, Senior Scientist, EFED

Executive Summary

The standard comparative analysis modeling technique often used in decision-analysis called the simple multi-attribute rating technique or SMART is adapted for comparing the risks of rodenticide baits based on a number of measures of effect values for primary and secondary risk to birds and mammals. Of the 11 rodenticide baits considered in the main document, three are considered to pose the greatest overall potential risk to birds and mammals: brodifacoum, zinc phosphide, and difethialone. Based on this analysis, brodifacoum poses the greatest potential risk to birds and mammals, and by a substantial margin over the other rodenticide baits. Brodifacoum has higher summary risk values than zinc phosphide for both secondary risk to birds and secondary risk to mammals. Zinc phosphide has higher summary risk values than difethialone for both primary risk to birds and primary risk to mammals.

A sensitivity analysis is performed to identify the most sensitive measure of effect(s) and to determine if changes of 50% or more in these sensitive measures of effect would change the results of the analysis. The results of this analysis show that the ranking for the rodenticide baits which pose the greatest potential risk to birds and mammals is robust when the measures of effect are changed by +/- 50%. The ranking is generally robust when the measures of effect are changed by +/- 99%, with the following exceptions: a reduction of greater than 67% in the Mean Dietary Risk Quotient for brodifacoum, 64% in the Mean (%) Mortality of Secondary Lab Studies on Birds for brodifacoum, and 76% in the Mean (%) Mortality of Secondary Lab Studies on Mammals for brodifacoum, would result in zinc phosphide moving ahead of brodifacoum as posing the greatest overall risk to birds and mammals; and, an increase of 99% in the Mean (%) Mortality of Secondary Lab Studies on Mammals for difethialone would result in difethialone moving ahead of zinc phosphide as posing the second greatest overall risk to birds and mammals. Thus, with few exceptions, the sensitivity analysis shows that brodifacoum poses the greatest overall potential risk to birds and mammals, followed by zinc phosphide and difethialone.

Acute toxicity reference values for rodenticides to birds and an alternative approach are also considered. The toxicity reference values from a recent publication are substituted for the avian LD50 values for bobwhite quail and mallard ducks used in one of the avian measures of effect for Primary Risk to Birds. The results show that the overall ranking remains the same and the use of these toxicity values does not affect the analysis. When unequal weighting of measures of effect for each type of risk is ignored and all measures of effect are considered together, again the results show that the overall ranking does not change. Unequal weighting of one type of risk over another, at least in this case, does not appear to have a significant effect on the overall ranking.

Two factors are identified as contributing the greatest uncertainty to the analysis: (1) missing data, especially secondary mortality data for difethialone, bromethalin, and cholecalciferol, and blood and liver retention values for a number of rodenticides; and (2) the assumption that field mortality to birds and mammals due to difethialone would likely equal 80% of that reported for brodifacoum. This assumption is based on the many chemical similarities between these two rodenticides, because difethialone bait is formulated at a lower % a.i. than brodifacoum, and the fact that compared to brodifacoum less difethialone is used.

The available incidents for birds and mammals are analyzed and compared to the summary of the weighted average risk values. The results confirm that brodifacoum is the rodenticide bait that poses the greatest potential overall risk to birds and mammals, but they also identify bromadiolone and zinc phosphide as potential concerns for birds, and bromadiolone, diphacinone (100 ppm), and chlorophacinone (100 ppm) as potential concerns for mammals.

Introduction

Comparative risk assessment can be a daunting process when risk assessors are faced with risks for a number of alternative pesticides covering multiple endpoints. When attempting to decide which pesticides present the greatest overall risk and having to consider many different endpoints that lead to a matrix of comparisons, many risk assessors rely on individual or group intuition. The inability to simultaneously track risk values assigned to multiple endpoints among many alternative pesticides as well as the varying importance of each to the assessment can easily result in paralysis (indecision).

The Agency attempted to address such situations in a December 1998 presentation to the Federal Insecticide, Fungicide and Rodenticide (FIFRA) Science Advisory Panel (SAP) titled, "*A Comparative Analysis of Ecological Risks from Pesticides and Their Use: Background, Methodology, Case Study*"[1]. The Panel noted the many scientific uncertainties in the method, yet agreed that it was a useful screening tool that provides a rough estimate of relative risk. The Panel also made a number of helpful suggestions to improve the utility of the methodology presented for use in comparative analyses of ecological risk from pesticides. There are, however, two recommendations that the panel thought critical for valid results: risk quotients - risk indices which are used to express risk from pesticides to nontarget organisms, should never be combined (added); and, a sensitivity analysis should always be included. Following this advice, no risk quotients or indices have been added together for this analysis, and a sensitivity analysis has been included. An early draft of this analysis was submitted for additional peer review by experts outside the Agency. Their comments and suggestions are very helpful and have also been incorporated, to the extent possible, into the updated analysis and this final report.

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[1] See http://www.epa.gov/scipoly/sap/1998/index.htm#december8

Endpoint and Data Selection

This comparative analysis of the potential risks from eleven rodenticide baits is based on the available primary and secondary toxicity data and persistence information for the nine rodenticides which are presented the main document *"Potential Risks of Nine Rodenticides to Birds and Nontarget Mammals: A Comparative Approach"*. Henceforth, this will be referred to as the "main document". These eleven baits are compared based on four types of risk: primary risk to birds, primary risk to mammals, secondary risk to birds, and secondary risk to mammals. Each type of risk is quantitatively evaluated by one to three measures of effect:

Type or Risk	Measures of Effect (ME)
Primary Risk to Birds	1) Mean Dietary Risk Quotient (RQ = the ppm ai in the rodenticide bait/LC50). See Table 29 in the main document. When more than one dietary RQ is available, the mean is calculated and used.
	2) Inverse of the No. of Bait Pellets Needed for 100-g Bird to Ingest LD50 Dose at a Single Feeding See Table 28 in the main document and the 'no. bait pellets' column under 100-g non-passerine. All > values are assumed to be = values.
Primary Risk to Mammals	1) Inverse of the No. of Bait Pellets Needed for 100-g Mammal to Ingest LD50 Dose at a Single Feeding See Table 31 in the main document and the 'no. bait pellets' column under 100-g rodent. All > values are assumed to be = values.
Secondary Risk to Birds	1) Mean % Mortality of Secondary Lab Studies (Birds). See Tables 11-12, 14-16, 18-19 in the main document and the '% dead' column. Missing data are not considered in the analysis. Difethialone is considered a special case due to it's similarity to brodifacoum. While missing data, it is given a % equal to 80% of that for brodifacoum. Bait specific data is not available; thus, where there are two baits (chlorophacinone, diphacinone), the % dead is applied to both baits. 2) Blood Retention Time (days). See Tables 13 and 17 in the main document and the 'Blood $t_{1/2}$' column. Missing data are not considered in the analysis. Where multiple half-lives existed, the mean is calculated and used. Bait specific data are not available; thus, where there are two

	baits (chlorophacinone, diphacinone), the half-life is applied to both baits.
	3) Liver retention Time (days). See Tables 13 and 17 in the main document and the ‘Liver $t_{1/2}$‘ column. Missing data are not considered in the analysis. Where multiple half-lives existed, the mean is calculated and used. Bait specific data is not available; thus, where there are two baits (chlorophacinone, diphacinone), the half-life is applied to both baits.
Secondary Risk to Mammals	1) Mean % Mortality of Secondary Lab Studies (Mammals). See Tables 20-27 in the main document and the ‘% dead’ column. Missing data are not considered in the analysis. Difethialone is considered a special case due to it’s similarity to brodifacoum. It is given a % equal to 80% of that for brodifacoum. Bait specific data is not available; thus, where there are two baits (chlorophacinone, diphacinone), the % dead is applied to both baits.
	2) Blood Retention Time (days). See Tables 13 and 17 in the main document and the ‘Blood $t_{1/2}$‘ column. Missing data are not considered in the analysis. Where multiple half-lives existed, the mean is calculated and used. Bait specific data is not available; thus, where there are two baits (chlorophacinone, diphacinone), the half-life is applied to both baits.
	3) Liver retention Time (days). See Tables 13 and 17 in the main document and the ‘Liver $t_{1/2}$‘ column. Missing data are not considered in the analysis. Where multiple half-lives existed, the mean is calculated and used. Bait specific data is not available; thus, where there are two baits (chlorophacinone, diphacinone), the half-life is applied to both baits.

Table 1 contains the data for each of the measures of effect used in the analysis.

Method & Approach[2]

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[2] Much of the software description is based on a software review by Len Tashman and Sara Munro, 1997.

During the 1998 SAP presentation, commercially available software called *DecideRight® (Version 1.2)*[3] was presented as an useful tool designed to aid comparative analysis and support decision-making. This user friendly software is designed primarily for use in business, but it can be applied to many situations where risk assessors and decision-makers must choose among alternatives when many factors must be considered. The underlying methodology used in the software is called the simple multi-attribute rating technique or SMART (Goodwin and Wright, 1998). This technique was developed approximately 30-years ago and has become a standard in decision modeling. When faced with a number of alternatives pesticide baits and a number of types of risk with measures of effect, SMART prescribes that (1) each alternative pesticide be rated on each measure of effect, (2) each measure of effect be assigned a measure of importance to the decision-maker, and (3) a summary score for each alternative pesticide be calculated as a weighted average of the ratings, where the weights represent the relative importance of the measure of effect for each type of potential risk. In the end, the higher the summary score, the higher the potential risk for that alternative pesticide. The result of this process has proved to be superior to the alternative of reliance on intuition.

SMART is not rooted in probability and ignores any interaction or correlation between criteria. The assigned ratings are assumed to be based on full knowledge of the type of risk. However, some uncertainty can be dealt with in the ratings by a sensitivity analysis. In this case, two scenarios are developed where the individual risk ratings are varied to see the effect on the overall ranking. This results of this analysis is included.

To begin, the problem must be formulated as a question. In this analysis, the question being asked is: "*Which of the 11 Rodenticide Baits Pose the Greatest Overall Risk to Birds and Mammals Based on their Primary and Secondary Risk Characteristics?*" The following basic equation is used to calculate the summary values for the risk comparison:

Equation 1.

$$\textbf{Summary Value}_{\text{(scale from 0 to 10)}} = \Sigma\,[(\mathbf{ME}_i)(\mathbf{ME}_{max})^{-1}]\,[(\mathbf{Weight})\,(\Sigma\mathbf{Weights})^{-1}]\,(10)$$

where $\mathbf{ME}_i$ is the measure of effect value for one of the eleven rodenticide baits and $\mathbf{ME}_{max}$ is the maximum ME for all rodenticide baits; **Weight** is the importance value placed on each measure of effect, with high = 10 to 6.67, medium = 6.68 to 3.33, and low = 3.34 to 0; and, Σ**Weights** is the sum of all the weights for all the measures of effect.

For this analysis, potential risk increased as all measures of effect values increased. For two measures: No. Bait Pellets Needed for 100-g Bird to Ingest LD50 Dose at a Single Feeding; and,

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[3] *DecideRight®* was developed by Avantos Performance Systems of Emertville, California. The company has since closed; however, the software is still available from Performance Management Solutions, LLC, 1198 Pacific Coast Hwy., D515 Seal Beach, CA. 90740 [Ph. 562/430-7096 Ext. 0 - Fax. 800/645-6618]. Also, see http://www.performancesolutionstech.com/default.htm . Mention of this commercial product does not constitute a recommendation or endorsement by EPA.

No. Bait Pellets Needed for 100-g Mammal to Ingest LD50 Dose at a Single Feeding, the inverse of the number of bait pellets was used in order to correctly calculate the weighted averages and avoid skewed results. Further, the weights given to all measures of effect are high (=10) since we did not have any scientific reason to differentiate between the importance of the measures, except for the two measures of retention or persistence in prey. The half-life in blood and liver are each given a weight of medium (2.5) for the secondary risk to birds and the secondary risk to mammals since we believe that the overall importance of the persistence should equal that of the mortality observed in the toxicity studies (2.5 x 4 = 10). Finally, summary values for each of the four risk types (i.e., primary risk to birds, primary risk to mammals, secondary risk to birds, secondary risk to mammals) are calculated separately and then these summary values are analyzed together in a final overall analysis. An alternate approach is considered where all measure of effects are considered in one step. The results of different approaches are compared and discussed later in this appendix. Basically, the approach using separate risk calculations is chosen because it eliminated unequal weighting of one risk over another due to differences in the number of measures of effect.

The *DecideRight*® software is not used for the analysis; rather, *Lotus SmartSuite 1-2-3*® is used for all calculations .

Table 1. Input Data for Comparative Analysis of Risk from 11 Rodenticide Baits

	Type of Risk								
	Primary Risk to Birds		*Primary Risk to Mammals*	*Secondary Risk to Birds*			*Secondary Risk to Mammals*		
	Measures of Effect		**Measure of Effect**	**Measures of Effect**			**Measures of Effect**		
Alternative Pesticides	**Mean Dietary Risk Quotient (ppm bait/LC50)**	**Inverse of the No. Bait Pellets Needed for 100gm Bird to Ingest LD50 Dose**	**Inverse of the No. Bait Pellets Needed for 100gm Mammal to Ingest LD50 Dose**	**Mean Mortality (%)of Secondary Lab Studies (Birds)**	**Blood Retention Time (days)**	**Liver Retention Time (days)**	**Mean Mortality (%) of Secondary Lab Studies (Mammals)**	**Blood Retention Time (days)**	**Liver Retention Time (days)**
Brodifacoum 50 ppm	**44.00**	**0.3846**	**0.25**	**42.00**	**7.30**	**217.00**	**42.00**	**7.30**	**217.00**
Bromadiolone 50 ppm	**0.85**	**0.0007**	**0.14**	**8.00**	**1.40**	**248.00**	**23.00**	**1.40**	**248.00**
Bromethalin 100 ppm	**0.35**	**0.0435**	**0.02**	**No Data**	**5.60**	**No Data**	**0.00**	**5.60**	**No Data**
Chlorophacinone 100 ppm	**1.20**	**0.0008**	**0.03**	**0.00**	**0.40**	**No Data**	**55.00**	**0.40**	**No Data**
Chlorophacinone 50 ppm	**0.60**	**0.0004**	**0.02**	**0.00**	**0.40**	**No Data**	**55.00**	**0.40**	**No Data**
Cholecalciferol 750 ppm	**1.00**	**0.0025**	**0.04**	**0.00**	**25.50**	**No Data**	**0.00**	**25.50**	**No Data**
Difethialone 25 ppm	**34.00**	**0.1923**	**0.09**	**33.60**	**2.50**	**117.70**	**33.60**	**2.50**	**117.70**
Diphacinone 100 ppm	**0.10**	**0.0005**	**0.09**	**9.00**	**17.50**	**90.00**	**58.00**	**17.50**	**90.00**
Diphacinone 50 ppm	**0.10**	**0.0003**	**0.04**	**9.00**	**17.50**	**90.00**	**58.0**	**17.50**	**90.00**
Warfarin 250 ppm	**0.35**	**0.0008**	**0.17**	**9.00**	**0.82**	**35.00**	**9.00**	**0.82**	**0.35.00**
Zinc Phosphide 20,000 ppm	**24.75**	**3.3333**	**2.00**	**0.00**	**No Data**	**No Data**	**4.00**	**No Data**	**No Data**

Results of the Comparative Analysis Model

As noted above, the summary values for each of the four risk types are calculated separately and then these summary values are analyzed together in a final overall analysis. Decision tables and graphs of the sums of the weighted averages for each of the four risk types are presented separately below. At the end, the decision table and graph for the overall potential risk analysis is presented.

By way of example, a detailed explanation of how the comparative analysis model results presented in Table 2. - Greatest Primary Risk to Birds - are calculated, is provided here in a series of steps. The measure of effect values come from Table 1.

Step 1. Give a Weight (Importance Value) to each Measure of Effect

Both Measures of Effect for Primary Risk to Birds are given a weight of high =10.

Step 2. Normalize the Assigned Weights for each Measure of Effect

Divide each weight by the sum of the all weights, i.e. 10/20 = 0.5, and multiply the result by 10. Thus, the weight for each Measure of Effect = 5.

Step 3. Calculate the Weighted Average Values for Each Measure of Effect and each Bait

Substep A. The first measure of effect is the Mean Dietary Risk Quotient (ppm bait/LC50). The calculation for each rodenticide bait is: The RQ value for that rodenticide is divided by the Maximum RQ value for all the rodenticides; and, the result is multiplied by the normalized wight for the measure of effect. Specifically, for each rodenticide bait, the calculations are as follows:

Brodifacoum 50 ppm: (44.0/44.0)*5 = 5.00
Bromadiolone 50 ppm: (0.85/44.0)*5 = 0.10
Bromethalin 100 ppm: (0.35/44.0)*5 = 0.04
Chlorophacinone 100 ppm: (1.20/44.0)*5 = 0.14
Chlorophacinone 50 ppm: (0.60/44.0)*5 = 0.07
Cholecalciferol 750 ppm: (1.00/44.0)*5 = 0.11
Difethialone 25 ppm: (34.0/44.0)*5 = 3.86
Diphacinone 100 ppm: (0.10/44.0)*5 = 0.01
Diphacinone 50 ppm: (0.10/44.0)*5 = 0.01
Warfarin 250 ppm: (0.35/44.0)*5 = 0.04
Zinc Phosphide 20,000 ppm: (24.75/44.0)*5 = 2.81

Substep B. The second measure of effect is the No. Bait Pellets Needed for a 100 g Bird to Ingest LD50 Dose at a Single Feeding. The inverse of this measure of effect was used in order to correctly calculate the weighted averages and avoid skewed results. The Inverse of the No. Bait Pellets value for each rodenticide is divided by the Maximum

Inverse of the No. Bait Pellets value; then, this result is multiplied by the normalized weight for the measure of effect. Specifically, for each rodenticide bait, the calculations are as follows:

Brodifacoum 50 ppm: (0.3846/3.3333)*5 = 0.58
Bromadiolone 50 ppm: (0.0007/3.3333)*5 = 0.00
Bromethalin 100 ppm: (0.0435/3.3333)*5 = 0.07
Chlorophacinone 100 ppm: (0.0008/3.3333)*5 = 0.00
Chlorophacinone 50 ppm: (0.0004/3.3333)*5 = 0.00
Cholecalciferol 750 ppm: (0.0025/3.3333)*5 = 0.00
Difethialone 25 ppm: (0.1923/3.3333)*5 = 0.29
Diphacinone 100 ppm: (0.0005/3.3333)*5 = 0.00
Diphacinone 50 ppm: (0.0003/3.3333)*5 = 0.00
Warfarin 250 ppm: (0.0008/3.3333)*5 = 0.00
Zinc Phosphide 20,000 ppm: (3.3333/3.3333)*5 = 5.00

Step 4. Sum the Weighted Average Values for Both Measures of Effect for each Rodenticide Bait

The weighted average values calculated above are summed for each rodenticide bait to arrive at the sum of the weighted average values for primary risk to birds.

Brodifacoum 50 ppm: 5.00+0.58 = 5.58
Bromadiolone 50 ppm: 0.10+0.00 = 0.10
Bromethalin 100 ppm: 0.04+0.07 = 0.10
Chlorophacinone 100 ppm: 0.14+0.00 = 0.14
Chlorophacinone 50 ppm: 0.07+0.00 = 0.07
Cholecalciferol 750 ppm: 0.11+0.00 = 0.12
Difethialone 25 ppm: 3.86+0.29 = 4.15
Diphacinone 100 ppm: 0.01+0.00 = 0.10
Diphacinone 50 ppm: 0.01+0.00 = 0.01
Warfarin 250 ppm: 0.04+0.00 = 0.04
Zinc Phosphide 20,000 ppm: 2.81+5.00 = 7.81

The summary values above, in ranked order from highest to lowest, are found in Table 2, and Figure 1 presents a graph of the calculations. Rounding affects some of the calculations.

Results of Comparative Analysis for Primary Risk to Birds

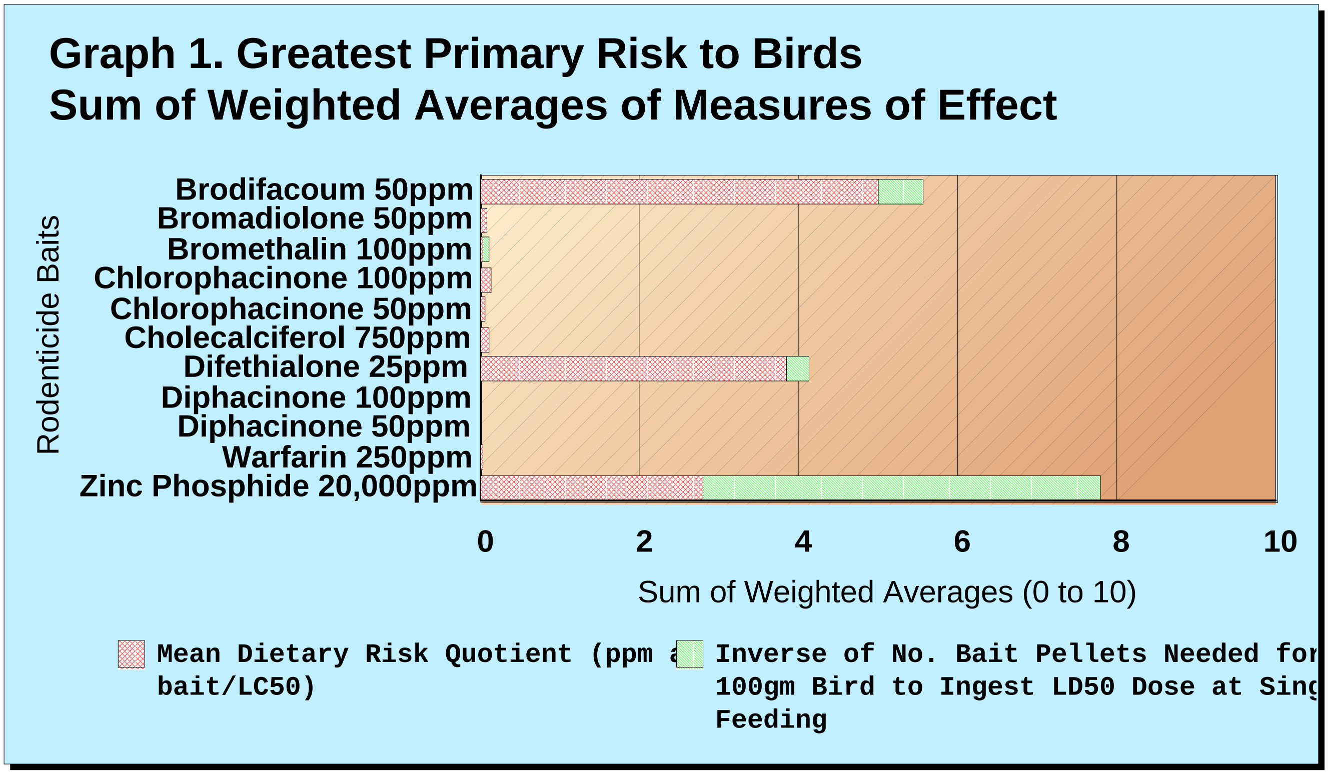
The question *"Which of the 11 Rodenticide Baits Pose the Greatest Primary Risk to Birds?"* is analyzed by the comparative model and the results are presented in a table (Table 2). The sum of the weighted average values for primary risk to birds is found in the ‘Summary Values” column in Table 2, and graphically shown in Figure 1. The results are based on two measures of effect: Mean Dietary Risk Quotient (ppm bait/LC50) and the Inverse of the No. Bait Pellets Needed for 100-g Bird to Ingest LD50 at Single Feeding. Of all the rodenticide baits considered, three are considered to pose the greatest potential primary risk to birds:

Zinc Phosphide 20,000 ppm
Brodifacoum 50 ppm
Difethialone 25 ppm

Based on this analysis, zinc phosphide poses the greatest potential primary risk to birds. The Inverse of the No. Bait Pellets Needed for 100-g Bird to Ingest LD50 at Single Feeding appears to be the most significant measure of effect leading to the conclusion that zinc phosphide poses greater risk to birds than brodifacoum. It also appears to be the most significant measure of effects leading to the conclusion that zinc phosphide poses greater potential primary risk to birds than difethialone. Brodifacoum has a higher summary risk value for one of the two measures of effect, mean dietary risk quotient (ppm ai bait/LC50), than both zinc phosphide and difethialone. Difethialone also has a higher summary risk value for one of the two measures of effect, mean dietary risk quotient (ppm ai bait/LC50), than zinc phosphide.

Table 2. Decision Table: Greatest Primary Risk to Birds.

	Mean Dietary Risk Quotient (ppm bait/ LC50)	*Inverse of No. Bait Pellets Needed for 100gm Bird to Ingest LD50 Dose at Single Feeding*	*Summary Values*
Alternative Pesticides	Measure of Effect Values		
Brodifacoum 50ppm	44.00	0.38	5.58
Bromadiolone 50ppm	0.85	0.00	0.10
Bromethalin 100ppm	0.35	0.04	0.10
Chlorophacinone 100ppm	1.20	0.00	0.14
Chlorophacinone 50ppm	0.60	0.00	0.07
Cholecalciferol 750ppm	1.00	0.00	0.12
Difethialone 25ppm	34.00	0.19	4.15
Diphacinone 100ppm	0.10	0.00	0.01
Diphacinone 50ppm	0.10	0.00	0.01
Warfarin 250ppm	0.35	0.00	0.04
Zinc Phosphide 20,000ppm	24.75	3.33	7.81



Graph 1. Greatest Primary Risk to Birds
Sum of Weighted Averages of Measures of Effect

Results of Comparative Analysis for Primary Risk to Mammals

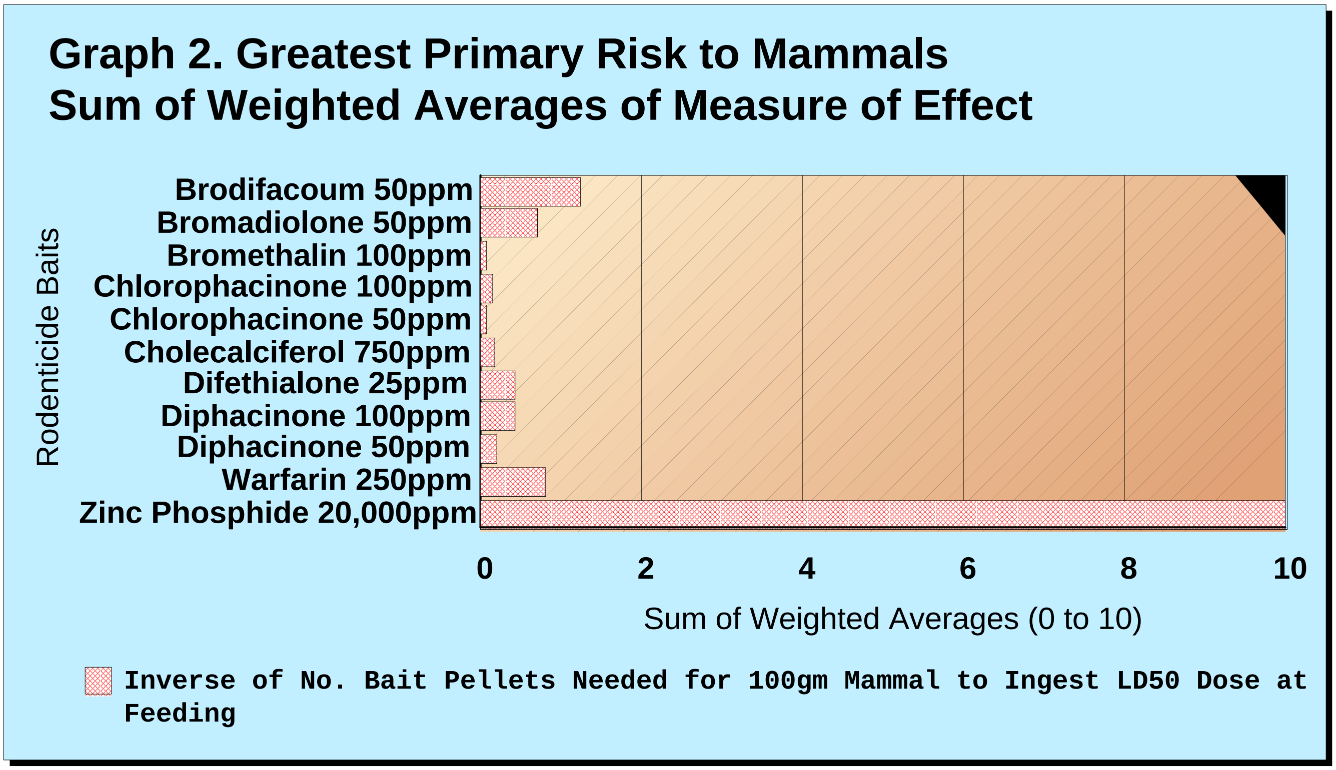
The question *"Which of the 11 Rodenticide Baits Pose the Greatest Primary Risk to Mammals?*" is analyzed by the comparative model and the results are presented in a table (Table 3). The sum of the weighted average values for primary risk is found in the 'Summary Values" column in Table 3, and graphically shown in Figure 2. The results are based on a single measure of effect: Inverse of the No. Bait Pellets Needed for 100-g Mammal to Ingest an LD50 Dose at a Single Feeding. Of all the rodenticide baits considered, one is considered to pose the greatest potential primary risk be mammals:

Zinc Phosphide 20,000 ppm

Based on this analysis, zinc phosphide poses the greatest potential primary risk to mammals by a substantial margin over the other rodenticide baits. Warfarin and brodifacoum are in distant second and third place.

Table 3. Greatest Primary Risk to Mammals.

	Inverse of No. Ba Pellets Needed for 100gm Mammal to Ingest LD50 Dose at Single Feeding	*Summary Values*
Alternative Pesticides	Measure of Effect Value	
Brodifacoum 50ppm	0.25	1.25
Bromadiolone 50ppm	0.14	0.71
Bromethalin 100ppm	0.02	0.10
Chlorophacinone 100ppm	0.03	0.16
Chlorophacinone 50ppm	0.02	0.08
Cholecalciferol 750ppm	0.04	0.18
Difethialone 25ppm	0.09	0.45
Diphacinone 100ppm	0.09	0.43
Diphacinone 50ppm	0.04	0.22
Warfarin 250ppm	0.17	0.83
Zinc Phosphide 20,000ppm	2.00	10.00



Graph 2. Greatest Primary Risk to Mammals
Sum of Weighted Averages of Measure of Effect

Results of Comparative Analysis for Secondary Risk to Birds

The question *"Which of the 11 Rodenticide Baits Pose the Greatest Secondary Risk to Birds ?"* is analyzed by the comparative model and the results are presented in a table (Table 4). The sum of the weighted average values for secondary risk to birds is found in the 'Summary Values" column in Table 4, and graphically shown in Figure 3. The results are based on three measures of effect: Mean % Mortality of Secondary Lab Studies, Blood Retention Time (Days), Liver Retention Time (Days). Of all the rodenticide baits considered, two are considered to pose the greatest potential secondary risk to birds:

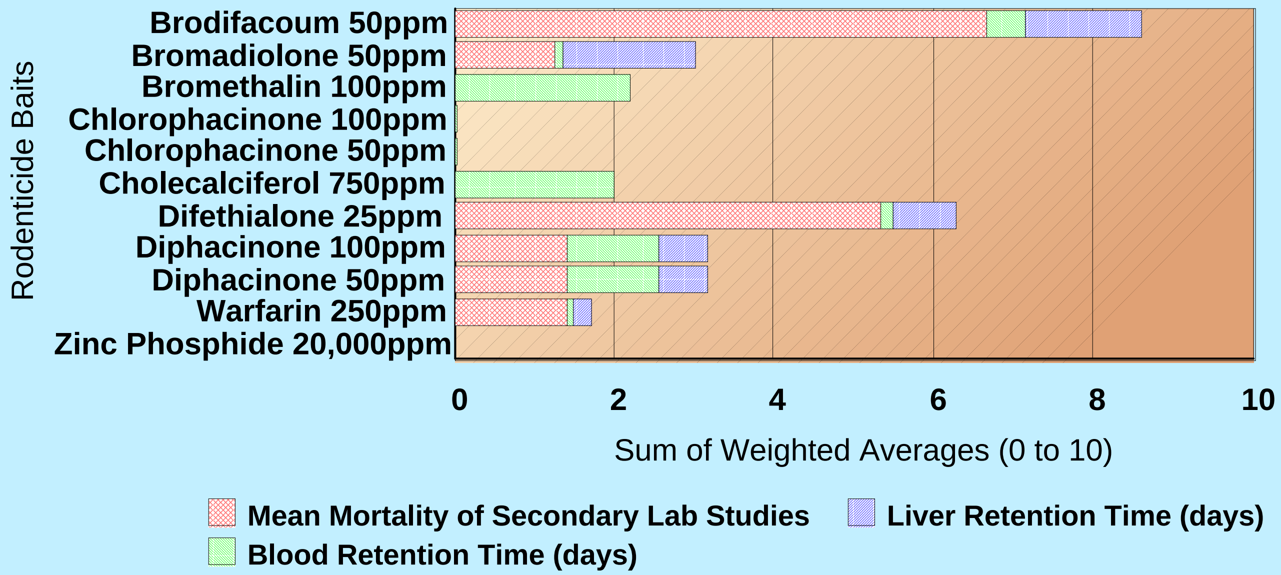
Brodifacoum 50 ppm
Difethialone 25 ppm

Based on this analysis, brodifacoum poses the greatest potential secondary risk to birds, and by a substantial margin over difethialone. Brodifacoum had higher summary values for all three measures of effect. Mean (%) Mortality of Secondary Lab Studies appears to be the most significant measure of effect leading to the conclusion that brodifacoum poses greater risk than difethialone.

Table 4. Greatest Secondary Risk to Birds.

	Mean Mortality of Secondary Lab Studies	Blood Retention Time (days)	Liver Retention Time (days)	*Summary Values*
Alternative Pesticides	Measures of Effect Value			
Brodifacoum 50ppm	42.00	7.30	217.00	8.60
Bromadiolone 50ppm	8.00	1.40	248.00	3.03
Bromethalin 100ppm	No Data	5.60	No Data	2.20
Chlorophacinone 100ppm	0.00	0.40	No Data	0.03
Chlorophacinone 50ppm	0.00	0.40	No Data	0.03
Cholecalciferol 750ppm	0.00	25.50	No Data	2.00
Difethialone 25ppm	33.60	2.50	117.70	6.29
Diphacinone 100ppm	9.00	17.50	90.00	3.18
Diphacinone 50ppm	9.00	17.50	90.00	3.18
Warfarin 250ppm	9.00	0.82	35.00	1.72
Zinc Phosphide 20,000ppm	0.00	No Data	No Data	0.00

Results of Comparative Analysis for Secondary Risk to Mammals



Graph 3. Greatest Secondary Risk to Birds
Sum of Weighted Averages of Measures of Effect

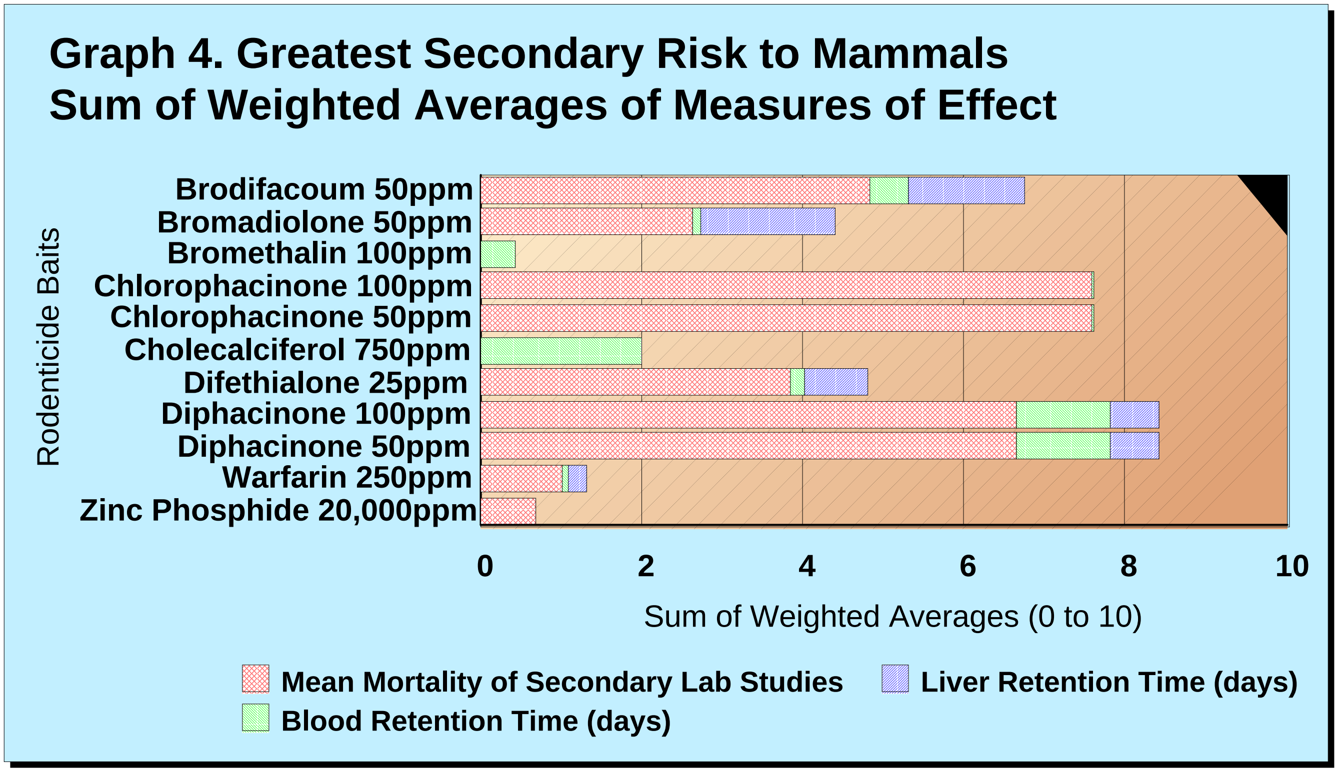
The question *"Which of the 11 Rodenticide Baits Pose the Greatest Secondary Risk to Mammals?"* is analyzed in the comparative analysis model and the results are presented in a table (Table 5). The sum of the weighted average values for secondary risk to mammals is found in the 'Summary Values" column in Table 5, and graphically shown in Figure 4. The results are based on three measures of effect: Mean % Mortality of Secondary Lab Studies, Blood Retention Time (Days), Liver Retention Time (Days). Of all the rodenticide baits considered, five are considered to pose the greatest potential secondary risk to mammals:

Diphacinone 100 ppm
Diphacinone 50 ppm
Chlorophacinone 100 ppm
Chlorophacinone 50 ppm
Brodifacoum 50 ppm

Based on this analysis, diphacinone (100 ppm and 50 ppm baits) pose the greatest potential secondary risk to mammals. Both rodenticide baits had identical summary risk values. Blood Retention Time (days) appears to be the most significant measure of effect leading to the conclusion that both of these diphacinone baits pose greater secondary risk to mammals than the chlorophacinone baits (100 ppm and 50 ppm baits). Both of the chlorophacinone baits had identical summary risk values as well. Mean (%) Mortality of Secondary Lab Studies appears to be the most significant measure of effect leading to the conclusion that both baits of diphacinone and chlorophacinone pose greater secondary risk to mammals than brodifacoum.

Table 5. Greatest Secondary Risk to Mammals.

	Mean Mortality of Secondary Lab Studies	Blood Retention Time (days)	Liver Retention Time (days)	*Summary Values*
Alternative Pesticides	Measures of Effect Value			
Brodifacoum 50ppm	42.00	7.30	217.00	6.76
Bromadiolone 50ppm	23.00	1.40	248.00	4.40
Bromethalin 100ppm	0.00	5.60	No Data	0.44
Chlorophacinone 100ppm	55.00	0.40	No Data	7.62
Chlorophacinone 50ppm	55.00	0.40	No Data	7.62
Cholecalciferol 750ppm	0.00	25.50	No Data	2.00
Difethialone 25ppm	33.60	2.50	117.70	4.82
Diphacinone 100ppm	58.00	17.50	90.00	8.42
Diphacinone 50ppm	58.00	17.50	90.00	8.42
Warfarin 250ppm	9.00	0.82	35.00	1.32
Zinc Phosphide 20,000ppm	4.00	No Data	No Data	0.69



Graph 4. Greatest Secondary Risk to Mammals
Sum of Weighted Averages of Measures of Effect

Results of Comparative Analysis for Overall Risk to Birds and Mammals

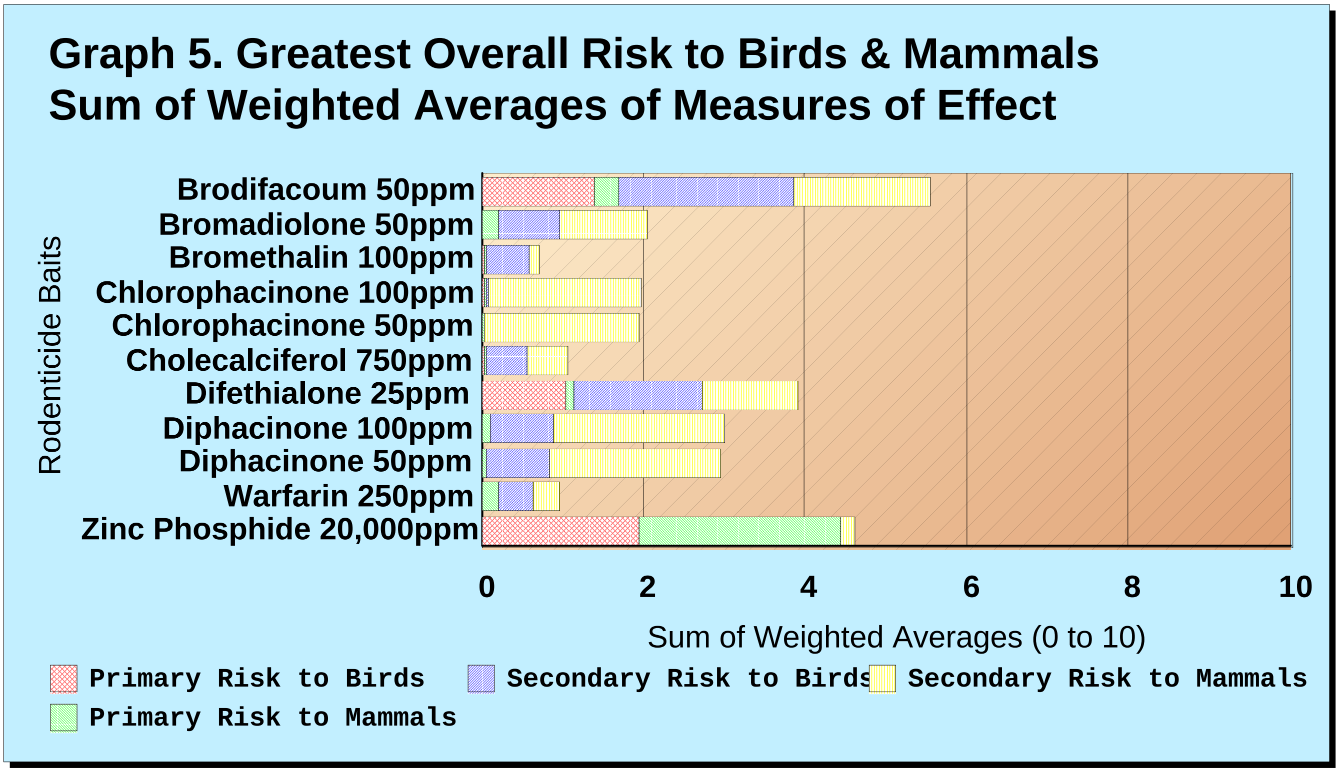
The question *"Which of the 11 Rodenticide Baits Pose the Greatest Overall Risk to Birds and Mammals?"* is analyzed by the comparative analysis model and the results are presented in a table (Table 6). The sum of the weighted average values for overall risk to birds and mammals is found in the 'Summary Values" column in Table 6, and graphically shown in Figure 5. The results are based on four types of risk, which in this case are the four measures of effect: Primary Risk to Birds, Primary Risk to Mammals, Secondary Risk to Birds, and Secondary Risk to Mammals. Of all the rodenticide baits considered, three are considered to pose the greatest potential overall risk to birds and mammals:

Brodifacoum 50 ppm
Zinc Phosphide 20,000 ppm
Difethialone 25 ppm

Based on this analysis, brodifacoum poses the greatest overall potential risk to birds and mammals and by a substantial margin over the other rodenticide baits. Brodifacoum has higher summary risk values than zinc phosphide for two of the four measures of effect. Secondary Risk to Birds and Secondary Risk to Mammals appear to be the most significant measures of effect leading to the conclusion that brodifacoum poses greater overall potential risk to birds and mammals than zinc phosphide. Zinc phosphide has higher summary risk values than difethialone for two of the four measures of effect, and Primary Risk to Mammals and Primary Risk to Birds appear to be the most significant measures of effect leading to the conclusion that zinc phosphide poses greater overall risk to birds and mammals than difethialone. Difethialone has higher summary risk values than both diphacinone baits (100 ppm and 50 ppm) for three of the four measures of effect, and Primary Risk to Birds appears to be the most significant measure of effect leading to the conclusion that difethialone poses greater overall potential risk to birds and mammals than both diphacinone baits.

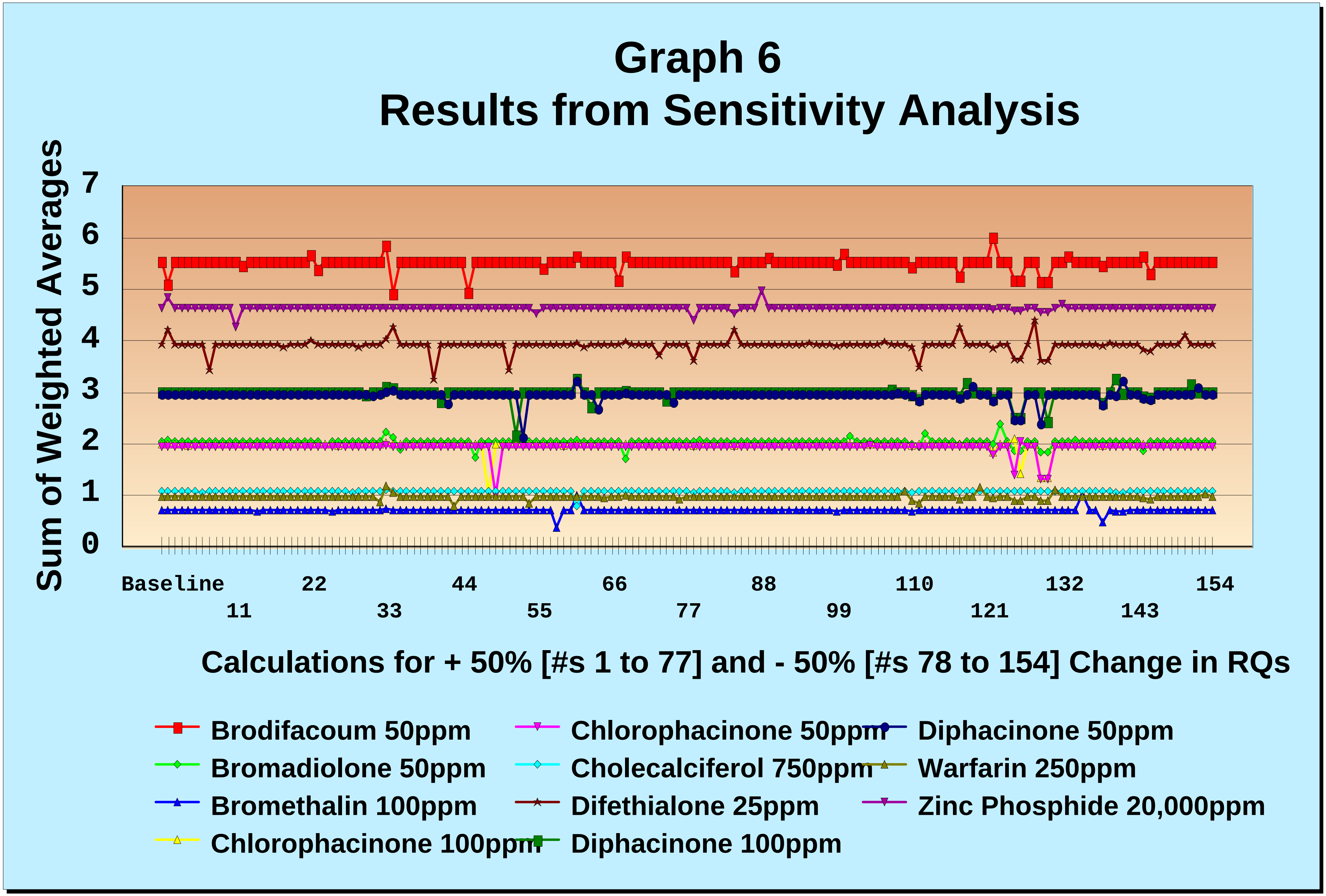
Table 6. Greatest Overall Risk to Birds and Mammals.

	Primary Risk to Birds	Primary Risk to Mammals	Secondary Risk to Birds	Secondary Risk to Mammals	***Summary Values***
Alternative Pesticides	Measures of Effect Value				
Brodifacoum 50ppm	5.58	1.25	8.60	6.76	5.55
Bromadiolone 50ppm	0.10	0.71	3.03	4.40	2.06
Bromethalin 100ppm	0.10	0.10	2.20	0.44	0.71
Chlorophacinone 100ppm	0.14	0.16	0.03	7.62	1.99
Chlorophacinone 50ppm	0.07	0.08	0.03	7.62	1.95
Cholecalciferol 750ppm	0.12	0.18	2.00	2.00	1.07
Difethialone 25ppm	4.15	0.45	6.29	4.82	3.93
Diphacinone 100ppm	0.01	0.43	3.18	8.42	3.01
Diphacinone 50ppm	0.01	0.22	3.18	8.42	2.96
Warfarin 250ppm	0.04	0.83	1.72	1.32	0.98
Zinc Phosphide 20,000ppm	7.81	10.00	0.00	0.69	4.63



Results of Sensitivity Analysis

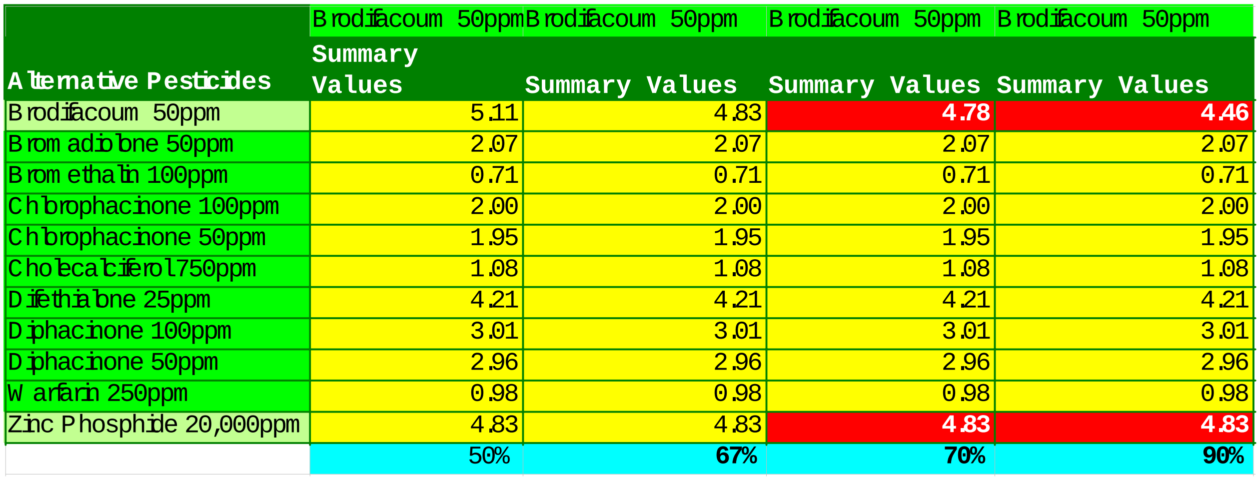
As previously noted, the FIFRA SAP recommended performing a sensitivity analysis. Specifically, they suggested that *“it would be useful to test the rankings by changing the values of the input variables...to lend insight to the robustness of the rankings, increase the confidence in the predictions, and move toward a better understanding of the effect that varying levels of uncertainty can have on the predictions.”* This is also a recommendation from a number of the peer reviewers. Therefore, to study how changes in each measure of effect value could affect the overall summary risk results presented above (Table 6 and Graph 5), a simple sensitivity analysis is performed using two scenarios: (1) vary each individual risk rating +50%, and -50%; and , (2) select certain risk rating that appeared to show a sensitivity to change, extend the change up to 90% (+ or -) or more. Thus, for the first scenario, each measure of effect value is separately decreased by 50%, and then increased by 50%. The percentage 50% is chosen arbitrarily, with the intention of choosing greater percentages for change in the second scenario after viewing these results. The changes in the overall summary risk values found in Table 6 as a result of the change in each measure of effect value, are recorded. The overall summary risk values in Table 6 are the baseline values. The results of the 154 changes in the summary risk values are presented in Graph 6.



Graph 6
Results from Sensitivity Analysis

With a 50 % (+ or -) change in the measure of effect values, the ranked positions for brodifacoum, zinc phosphide, and difethialone do not change, indicating that the ranking is robust at this level of change. However, the ranked positions of the other rodenticide baits change numerous times, as indicated by the numerous times the lines cross each other. A few of the changes do result in lower values for brodifacoum, such as #s 1, 34, 45 and 67, or higher values for zinc phosphide, such as #s 1 and 88, or higher values for difethialone, such as # 128. To further test the rankings, the measures of effect values for these numbers are increased to 90% (+ or -) or greater and the resultant overall summary risk values are presented below:

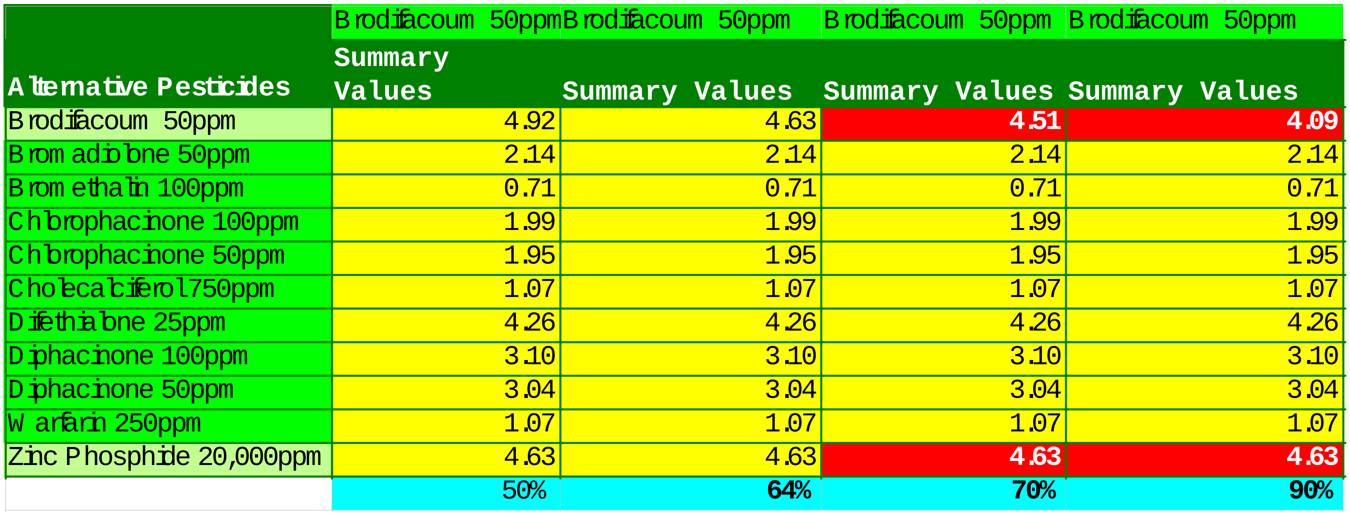
> #1, Reduction in the Mean Dietary Risk Quotient (ppm bait/LC50), one measure of effect for primary risk to birds for brodifacoum, of 50%, 67%, 70% and 90% resulted in the following ranking of overall summary risk values:



	Brodifacoum 50ppm	Brodifacoum 50ppm	Brodifacoum 50ppm	Brodifacoum 50ppm
Alternative Pesticides	**Summary Values**	**Summary Values**	**Summary Values**	**Summary Values**
Brodifacoum 50ppm	5.11	4.83	**4.78**	**4.46**
Bromadiolone 50ppm	2.07	2.07	2.07	2.07
Bromethalin 100ppm	0.71	0.71	0.71	0.71
Chlorophacinone 100ppm	2.00	2.00	2.00	2.00
Chlorophacinone 50ppm	1.95	1.95	1.95	1.95
Cholecalciferol 750ppm	1.08	1.08	1.08	1.08
Difethialone 25ppm	4.21	4.21	4.21	4.21
Diphacinone 100ppm	3.01	3.01	3.01	3.01
Diphacinone 50ppm	2.96	2.96	2.96	2.96
Warfarin 250ppm	0.98	0.98	0.98	0.98
Zinc Phosphide 20,000ppm	4.83	4.83	**4.83**	**4.83**
	50%	**67%**	**70%**	**90%**

> Results: A reduction in the Mean Dietary Risk Quotient, one of two measures of effect for primary risk to birds for brodifacoum, of greater than 67% would result in zinc phosphide moving ahead of brodifacoum as the rodenticide bait posing the greatest overall potential risk to birds and mammals.

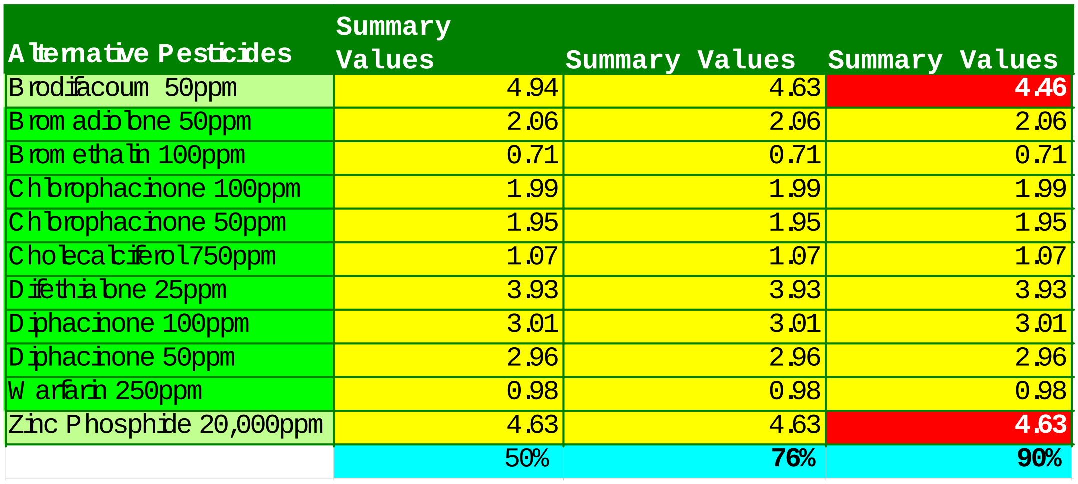
> #34, Reduction in the Mean (%) Mortality of secondary Lab Studies on Birds, one measure of effect for secondary risk to birds for brodifacoum, of 50%, 64%, 70 and 90%, resulted in the following ranking of overall summary risk values:



Alternative Pesticides	Brodifacoum 50ppm Summary Values	Brodifacoum 50ppm Summary Values	Brodifacoum 50ppm Summary Values	Brodifacoum 50ppm Summary Values
Brodifacoum 50ppm	4.92	4.63	4.51	4.09
Bromadiolone 50ppm	2.14	2.14	2.14	2.14
Bromethalin 100ppm	0.71	0.71	0.71	0.71
Chlorophacinone 100ppm	1.99	1.99	1.99	1.99
Chlorophacinone 50ppm	1.95	1.95	1.95	1.95
Cholecalciferol 750ppm	1.07	1.07	1.07	1.07
Difethialone 25ppm	4.26	4.26	4.26	4.26
Diphacinone 100ppm	3.10	3.10	3.10	3.10
Diphacinone 50ppm	3.04	3.04	3.04	3.04
Warfarin 250ppm	1.07	1.07	1.07	1.07
Zinc Phosphide 20,000ppm	4.63	4.63	4.63	4.63
	50%	64%	70%	90%

<u>Results</u>: A reduction in the Mean (%) Mortality of Secondary Lab Studies on Birds, one of two measures of effect for secondary risk to birds for brodifacoum, of greater than 64% would result in zinc phosphide moving ahead of brodifacoum as the rodenticide bait posing the greatest overall potential risk to birds and mammals.

#45, Reduction in the Mean (%) Mortality of secondary Lab Studies on Mammals, one measure of effect for secondary risk to mammals for brodifacoum, of 50%, 76% and 90%, resulted in the following ranking of overall summary risk values:

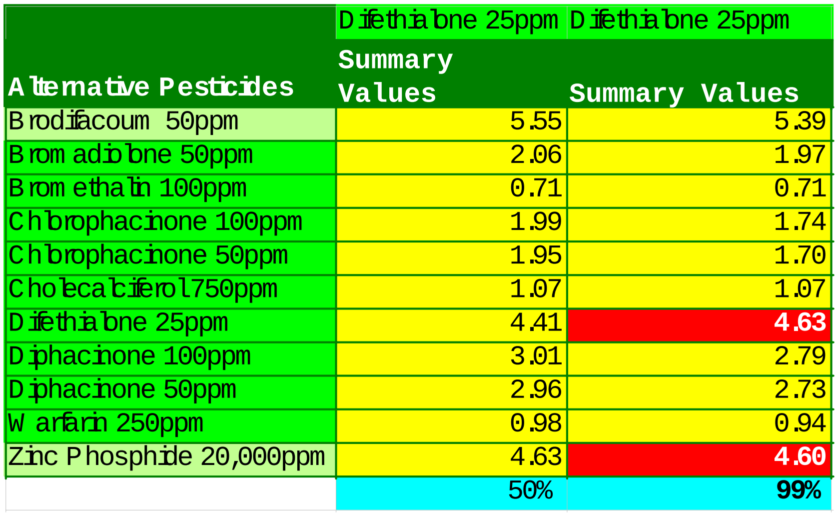


Alternative Pesticides	Summary Values	Summary Values	Summary Values
Brodifacoum 50ppm	4.94	4.63	4.46
Bromadiolone 50ppm	2.06	2.06	2.06
Bromethalin 100ppm	0.71	0.71	0.71
Chlorophacinone 100ppm	1.99	1.99	1.99
Chlorophacinone 50ppm	1.95	1.95	1.95
Cholecalciferol 750ppm	1.07	1.07	1.07
Difethialone 25ppm	3.93	3.93	3.93
Diphacinone 100ppm	3.01	3.01	3.01
Diphacinone 50ppm	2.96	2.96	2.96
Warfarin 250ppm	0.98	0.98	0.98
Zinc Phosphide 20,000ppm	4.63	4.63	4.63
	50%	76%	90%

<u>Results</u>: A reduction in the Mean (%) Mortality of Secondary Lab Studies on Mammals, one of two measures of effect for secondary risk to mammals for brodifacoum, of greater

than 76% would result in zinc phosphide moving ahead of brodifacoum as the rodenticide bait posing the greatest overall potential risk to birds and mammals.

#128, Increase in the Mean (%) Mortality of secondary Lab Studies on Mammals, one measure of effect for secondary risk to mammals for difethialone, of 50% and 99%, resulted in the following ranking of overall summary risk values:



	Difethialone 25ppm	Difethialone 25ppm
Alternative Pesticides	**Summary Values**	**Summary Values**
Brodifacoum 50ppm	5.55	5.39
Bromadiolone 50ppm	2.06	1.97
Bromethalin 100ppm	0.71	0.71
Chlorophacinone 100ppm	1.99	1.74
Chlorophacinone 50ppm	1.95	1.70
Cholecalciferol 750ppm	1.07	1.07
Difethialone 25ppm	4.41	**4.63**
Diphacinone 100ppm	3.01	2.79
Diphacinone 50ppm	2.96	2.73
Warfarin 250ppm	0.98	0.94
Zinc Phosphide 20,000ppm	4.63	**4.60**
	50%	**99%**

<u>Results</u>: An increase in the Mean (%) Mortality of Secondary Lab Studies on Rodents, one of two measures of effect for secondary risk to mammals for difethialone, of 99% would result in difethialone moving ahead of zinc phosphide as the rodenticide bait posing the second greatest overall potential risk to birds and mammals.

None of the following changes resulted in changes in rankings of brodifacoum, zinc phosphide or difethialone: a 99% reduction in Liver Retention Time (days) for brodifacoum (#67); a 99% increase in the Mean Avian Dietary Risk Quotient for zinc phosphide (#88); a 99% increase in the Mean (%) Mortality of secondary Lab Studies on Mammals for difethialone.

The sensitivity analysis shows that the ranking for the rodenticide baits which pose the greatest potential risk to birds and mammals is robust when the measures of effect are changed by +/- 50%. The ranking is generally robust when the measures of effect are changed by +/- 99%. However, a reduction of greater than 67% in the Mean Dietary Risk Quotient for brodifacoum, 64% in the Mean (%) Mortality of Secondary Lab Studies on Birds for brodifacoum, and 76% in the Mean (%) Mortality of Secondary Lab Studies on Mammals f or brodifacoum, would result in zinc phosphide moving ahead of brodifacoum as posing the greatest overall risk to birds and mammals. In addition, an increase of 99% in the Mean (%) Mortality of Secondary Lab Studies on Mammals for difethialone would result in difethialone moving ahead of zinc phosphide as posing the second greatest overall risk to birds and mammals. Thus, the sensitivity analysis shows that the ranking for the rodenticide baits is generally robust. With few exceptions we can confidently say that brodifacoum poses the greatest overall potential risk to birds and mammals, followed by zinc phosphide and difethialone.

Results Using Toxicity Reference Values for Birds

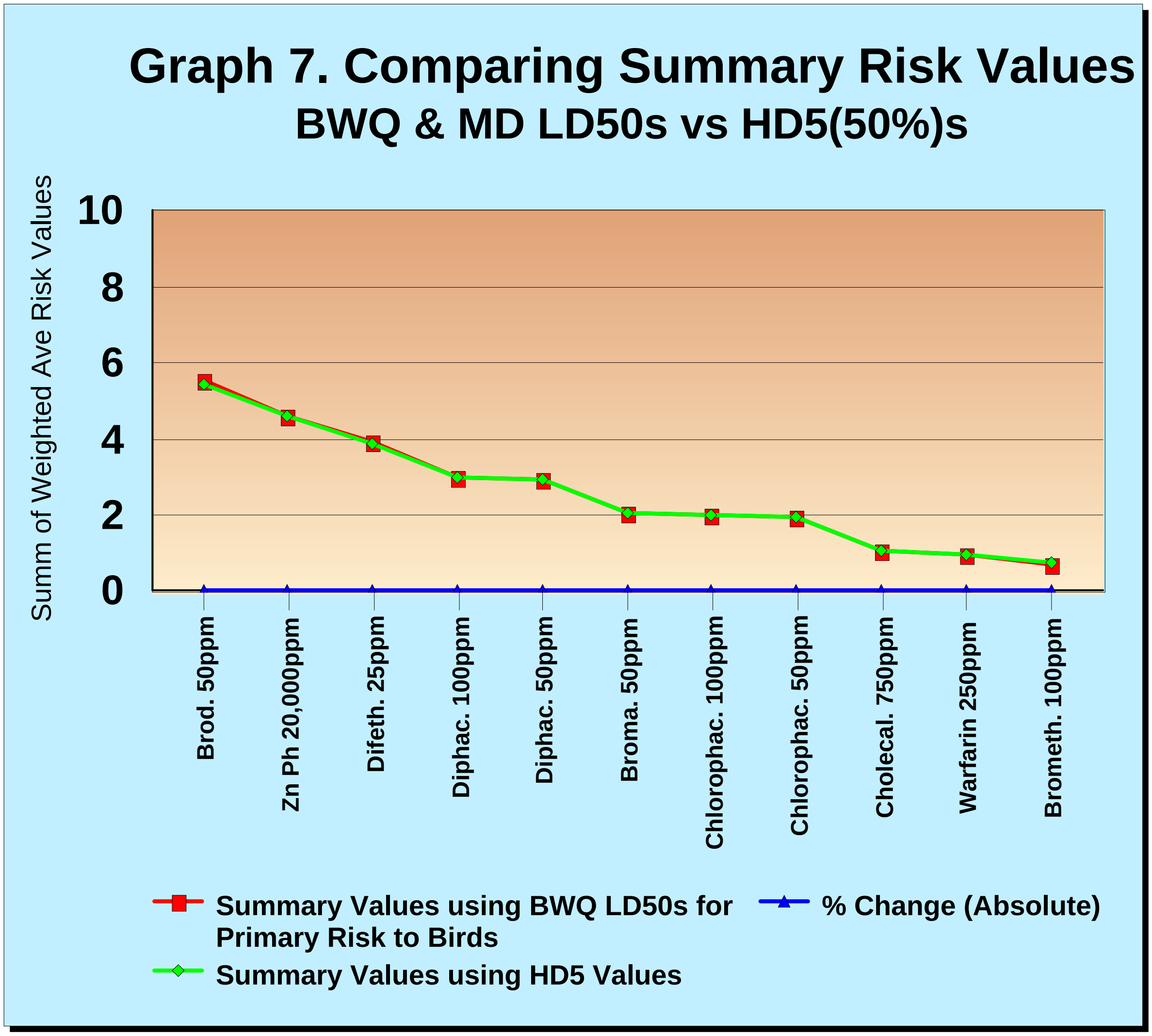
Mineau *et al* (2001) state that *"when carrying out comparative assessments for pesticides, it is essential to use the most unbiased data possible."* They suggest a distribution approach for avian LD50 data, modified (1) to incorporate body-weight scaling, and (2) to use extrapolation factors for pesticides for which there are insufficient data from which to derive a distribution. *"A distribution-based approach uses the pesticide-specific data available to define the shape of the distribution through the estimation of a mean and variance for the distribution."* As the authors note, *"Working with a distribution allows one to set a desired percentile, or threshold LD50 value sufficiently protective for an arbitrarily chosen portion of the entire population of bird species."* They follow other authors and arbitrarily set the protection level at the 5th percentile of the species distribution, which they term the Hazardous Dose 5% or HD_5. Further, they fixed the level of certainty at 50%. Thus, the HD_5(50%) reference value is the 5% tail of the avian LD50 toxicity distribution calculated with 50% probability of overestimation. They believe that this *"approach of using reference values based on species specific extrapolation factors represents the most unbiased attempt to date to compare the toxicity of pesticides for which many data points are available with those about which we know very little."*

Since HD_5(50%) reference values are available for all rodenticides but diphacinone (Table 3 in Mineau *et al*), these values are substituted for the LD50 values for bobwhite quail or mallard duck used in the measure of effect - Inverse the No. Bait Pellets Needed for a 100-g Bird LD50 Dose at a Single Feeding in the comparative analysis for Primary Risk to Birds.

Rodenticide	HD_5(50%)
Brodifacoum 50 ppm	0.81
Bromadiolone 50 ppm	53.26
Bromethalin 100 ppm	0.83
Chlorophacinone 100 ppm	3.32
Chlorophacinone 50 ppm	4.98
Cholecalciferol 750 ppm	192.68
Difethialone 25 ppm	0.31
Diphacinone 100 ppm	No Data
Diphacinone 50 ppm	No Data
Warfarin 250 ppm	120.21
Zinc Phosphide 20,000 ppm	5.45

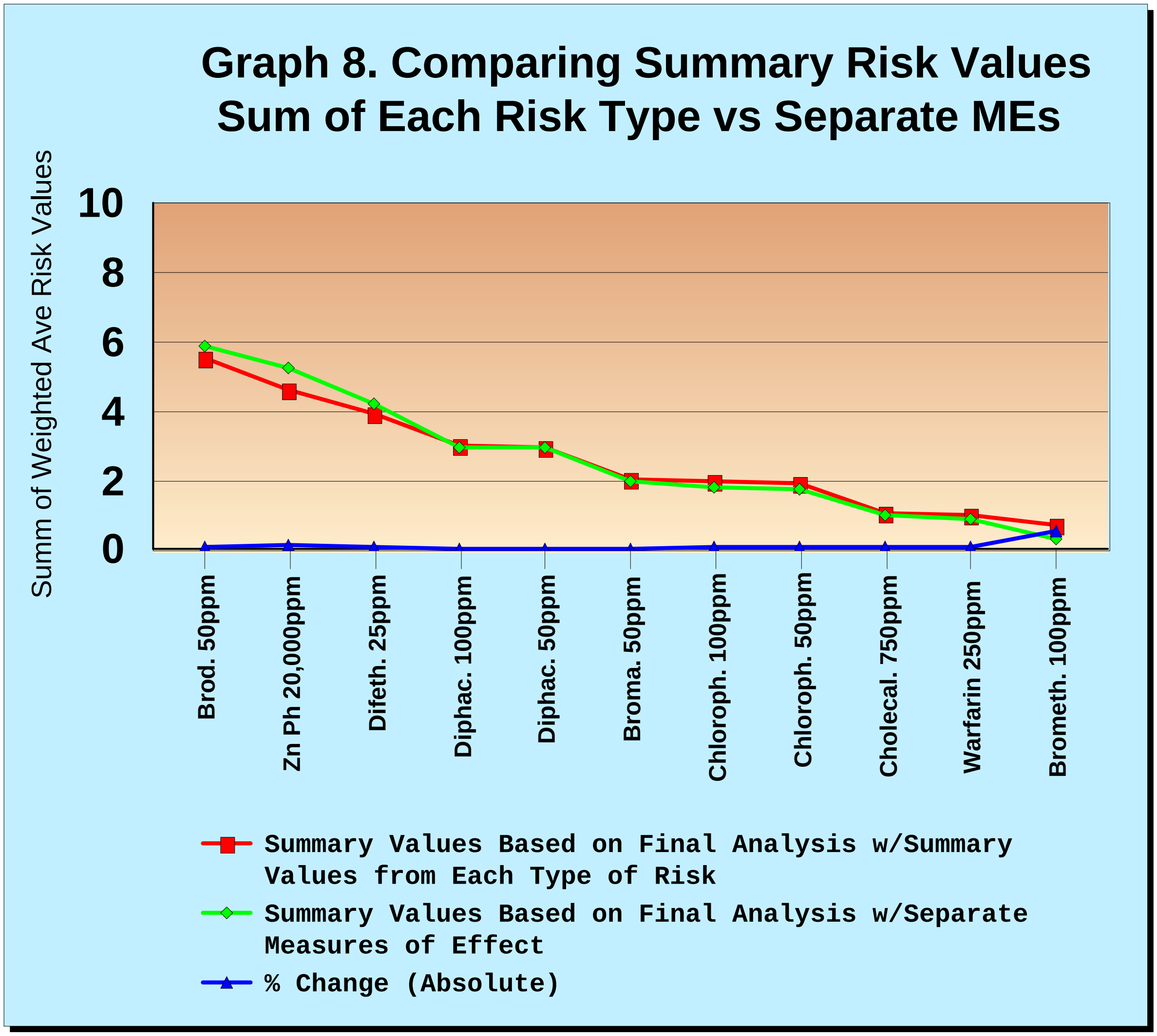
Since bait-specific HD_5(50%)s are not available, the HD_5(50%) value from Mineau *et al* is applied to the highest active ingredient concentration of two baits, and it is reduced by the proportion difference in active ingredient concentrations between baits and applied to the bait with the lower active ingredient concentration. Lacking slope data, this assumes a linear relationship between the active ingredient in the bait and the acute toxicity to birds. Finally, the overall summary values for risk to birds and mammals are calculated and compared to the baseline in Table 6 and Graph 5. The results of the analysis are presented in Graph 7.

This analysis shows that the ranking remains the same and the use of the HD_5(50%) values from Mineau *et al* in place of the LD50 values for bobwhite quail or mallard duck does not have any affect on ranking of the rodenticide baits posing the greatest overall potential risk to birds and mammals. Missing HD_5(50%)data for diphacinone adds uncertainty to this conclusion.


Graph 7. Comparing Summary Risk Values
BWQ & MD LD50s vs HD5(50%)s

As noted previously, the approach taken for this analysis is to separately analyze the risk for each risk type, then analyze the summary values for each of the four risk types together in a final overall analysis. Each type of risk included variable and unequal numbers of measures of effect. Analyzing them separately and then using their summary values to arrive at an overall risk value eliminated unequal weighting of one type of risk over another due to differences in the number of measures of effect.

An alternate approach is considered where the unequal weighting is ignored and all measure of effects are considered in one step. The weights are all rated high (10.0), except for blood retention and liver retention, which are weighted medium (5.0) so that the total contribution of persistence is rated equal to the other measures of effect (10.0). The overall summary risk values are calculated and compared to the baseline results in Table 5 and Graph 6. The results of this analysis is presented in Graph 8. The rankings for overall risk to birds and mammals do not change. Thus in this case, the unequal weighting of one type of risk over another due to differences in the number of measures of effect does not appear to have a significant effect on the overall ranking.



Graph 8. Comparing Summary Risk Values
Sum of Each Risk Type vs Separate MEs

Incidents

Bird and mammal incidents provide additional information to further characterize the risk of rodenticide baits. The collection and reporting of incidents is not systematic, and the presence or absence of incidents is also affected by the extent of use of the rodenticide bait as well as other factors. Thus, the existence of incidents for a rodenticide bait can be viewed as confirming the risk, where as the absence of them says little about the risk. Further, without more information than is typically available for most incident reports, it can sometimes be difficult to separate the incidents based on primary or secondary effects.

Based on Table 42 in the main document, there are a large number of bird and mammal incidents reported for rodenticide baits (161 birds; 119 mammal; 280 total). Reported mortality is attributed to both primary and secondary effects. The incidents reported for each rodenticide bait (where two baits are included in the analysis, the one with the highest concentration in the bait formulation is used) are plotted on the x-axis against the summary values of the weighted averages for the overall risk to birds and mammals (See summary values, Table 6) on the y-axis. The incidents are ‘turned around’ so that the rodenticide baits with the greatest number of reported incidents and the largest summary risk values should appear in the upper left of the graph. Tables 7, 8 and 9 show the input values for the following graphs. Graph 9 presents the bird incidents; Graph 10, the mammal incidents; and Graph 11, both combined.

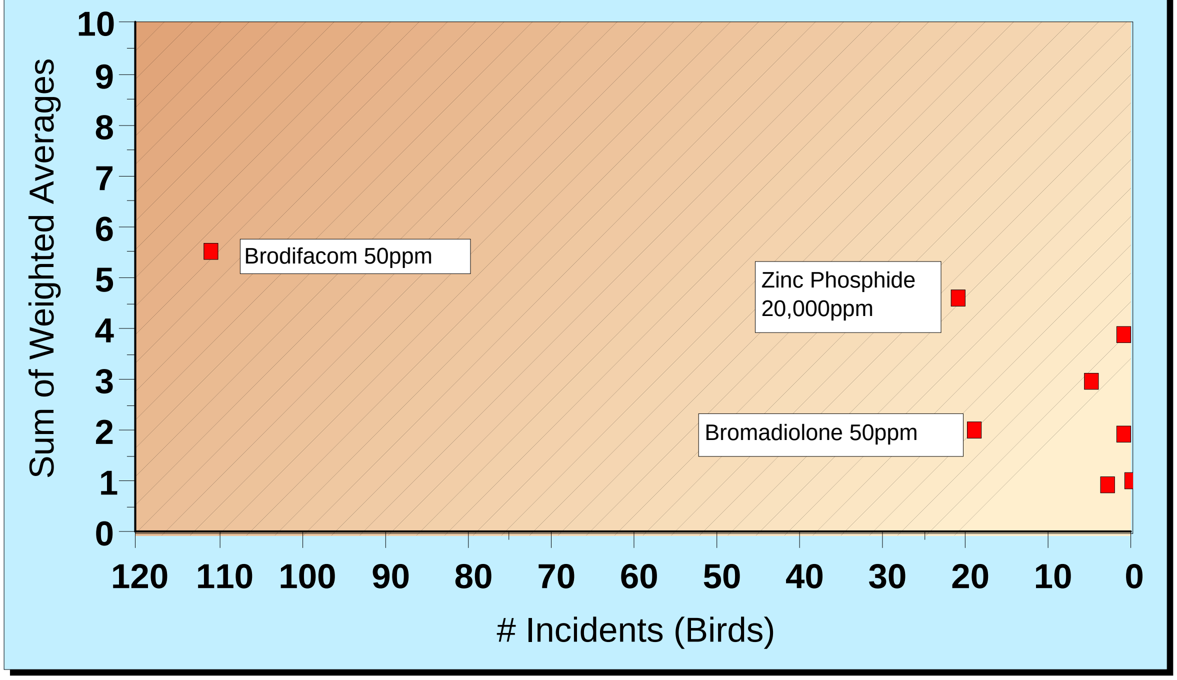
The graphs confirm that brodifacoum is the rodenticide bait that poses the greatest overall potential risk to birds and mammals. In addition to brodifacoum, Graph 9 also identifies bromadiolone and zinc phosphide as potential concerns for birds, while Graph 10 identifies bromadiolone, diphacinone, and chlorophacinone as potential risk concerns for mammals.

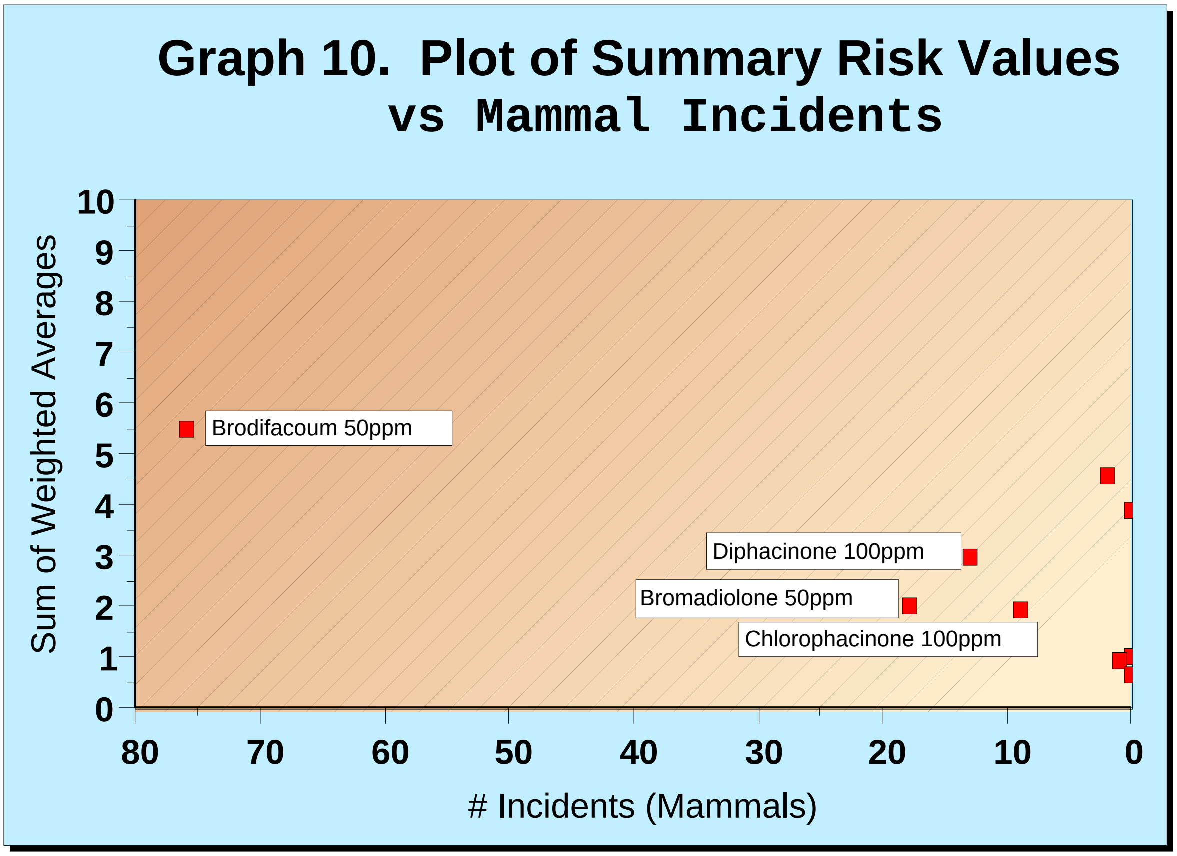
Table 7. Input values for Graph 9	# Incidents - Birds	Summary Values
Brodifacoum 50ppm	111	5.55
Zinc Phosphide 20,000ppm	21	4.63
Difethialone 25ppm	1	3.93
Diphacinone 100ppm	5	3.01
Bromadiolone 50ppm	19	2.06
Chlorophacinone 100ppm	1	1.99
Cholecalciferol 750ppm	0	1.07
Warfarin 250ppm	3	0.98
Bromethalin 100ppm	0	0.71
Sum	161	

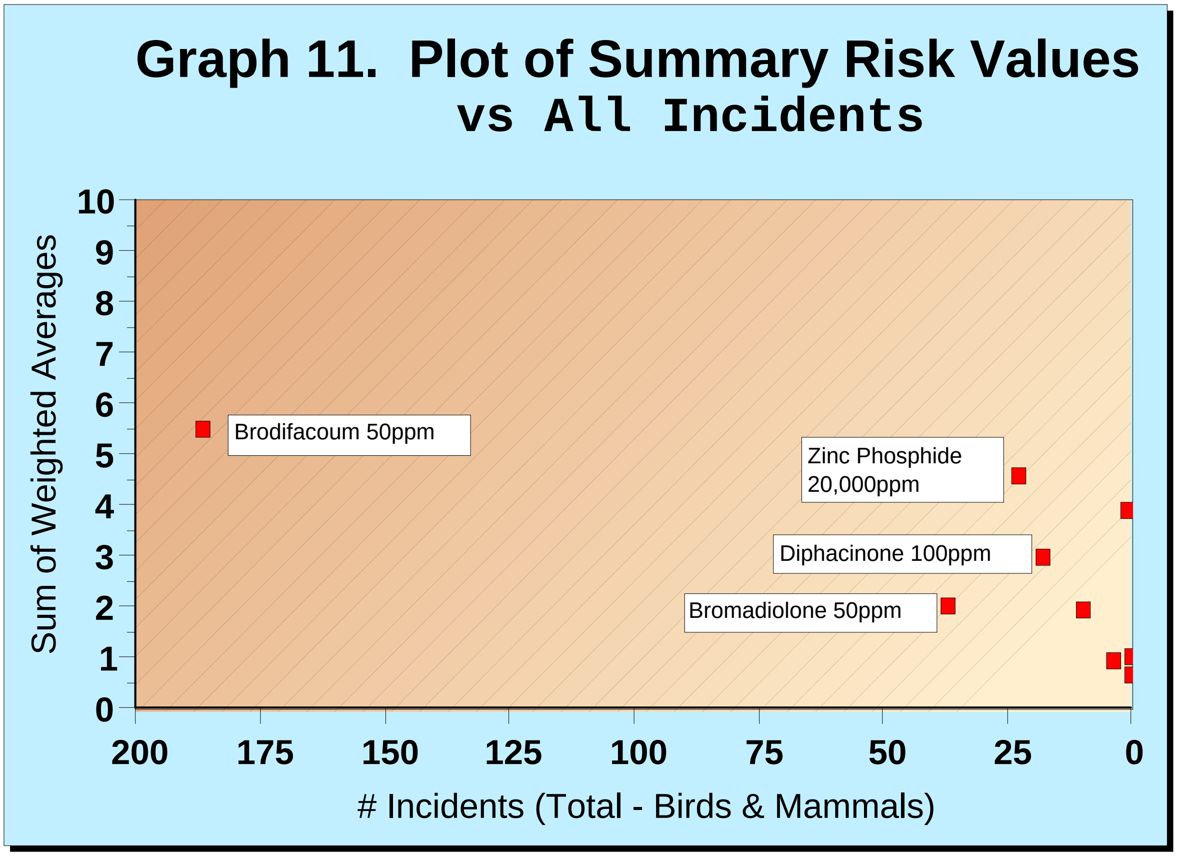
Table 8. Input Values for Graph 10.	# Incidents - Mammals	Summary Values
Brodifacoum 50ppm	76	5.55
Zinc Phosphide 20,000ppm	2	4.63
Difethialone 25ppm	0	3.93
Diphacinone 100ppm	13	3.01
Bromadiolone 50ppm	18	2.06
Chlorophacinone 100ppm	9	1.99
Cholecalciferol750ppm	0	1.07
Warfarin 250ppm	1	0.98
Bromethalin 100ppm	0	0.71
Sum	119	

Table 9. Input Values for Graph 11.	# Incidents - Total	Summary Values
Brodifacoum 50ppm	187	5.55
Zinc Phosphide 20,000ppm	23	4.63
Difethialone 25ppm	1	3.93
Diphacinone 100ppm	18	3.01
Bromadiolone 50ppm	37	2.06
Chlorophacinone 100ppm	10	1.99
Cholecalciferol750ppm	0	1.07
Warfarin 250ppm	4	0.98
Bromethalin 100ppm	0	0.71
Sum	280	

Graph 9. Plot of Summary Risk Values vs Birds Incidents




Graph 10. Plot of Summary Risk Values
vs Mammal Incidents
Sum of Weighted Averages
10
9
8
7
6
5
4
3
2
1
0
80
70
60
50
40
30
20
10
0
Incidents (Mammals)
Brodifacoum 50ppm
Diphacinone 100ppm
Bromadiolone 50ppm
Chlorophacinone 100ppm



Graph 11. Plot of Summary Risk Values vs All Incidents

Conclusions

Based on the comparative analysis model called the simple multi-attribute rating technique or SMART, the potential risks of 11 rodenticide baits are compared based on a number of measures of effect values for primary and secondary risk to birds and mammals. Of all the rodenticide baits considered, three are considered to pose the greatest overall potential risk to birds and mammals: brodifacoum, zinc phosphide, and difethialone. Brodifacoum poses the greatest overall potential risk to birds and mammals, and by a substantial margin over the other rodenticide baits. Brodifacoum has higher summary risk values than zinc phosphide for both secondary risk to birds and secondary risk to mammals. Zinc phosphide has higher summary risk values than difethialone for both primary risk to birds and primary risk to mammals.

A sensitivity analysis is performed to identify the most sensitive measure of effect(s) and to determine if changes of 50% or more in these sensitive measures of effect would change the results of the analysis. This analysis shows that the ranking for the rodenticide baits which pose the greatest risk to birds and mammals is robust when the measures of effect are changed by +/- 50%. The ranking is generally robust when the measures of effect are changed by +/- 99%, with the following exceptions: a reduction of greater than 67% in the Mean Dietary Risk Quotient for brodifacoum, 64% in the Mean (%) Mortality of Secondary Lab Studies on Birds for brodifacoum, and 76% in the Mean (%) Mortality of Secondary Lab Studies on Mammals for brodifacoum, would result in zinc phosphide moving ahead of brodifacoum as posing the greatest overall risk to birds and mammals; and, an increase of 99% in the Mean (%) Mortality of Secondary Lab Studies on Mammals for difethialone would result in difethialone moving ahead of zinc phosphide as posing the second greatest overall potential risk to birds and mammals. Thus, the sensitivity analysis shows that the ranking for the rodenticide baits is generally robust. With few exceptions, we can say that brodifacoum poses the greatest overall potential risk to birds and mammals, followed by zinc phosphide and difethialone.

Acute toxicity reference values for rodenticides to birds and an alternative approach are also considered. The toxicity reference values from a recent publication are substituted for the avian LD50 values for bobwhite quail and mallard ducks that were used in one of the avian measures of effect. The results show that the overall ranking remains the same and the use of these toxicity reference values do not affect the analysis. When unequal weighting of measures of effect for each type of risk is ignored and all measures of effect are considered together, again the results show that the overall ranking does not change. Unequal weighting of type of risk over another, in this case, does not appear to have a significant effect on the overall ranking.

There are two factors which could contribute the greatest uncertainty to the analysis: (1) missing data, especially field mortality data for difethialone, and blood and liver retention values for a number of rodenticides; and (2) the assumption that field mortality to birds and mammals due to difethialone would likely equal 80% of that reported for brodifacoum. This assumption is based on the many chemical similarities between these two rodenticides, because difethialone is formulated at a lower % ai than brodifacoum, and the fact that less difethialone is used compared to brodifacoum.

The available incidents for birds and mammals are analyzed and compared the summary of the weighted average risk values. The results confirm that brodifacoum is the rodenticide bait that poses the greatest overall potential risk to birds and mammals, but they also identify bromadiolone and zinc phosphide as potential concerns for birds, and bromadiolone, diphacinone (100 ppm), and chlorophacinone (100 ppm) as potential concerns for mammals.

References

1. Tashman, L. and S. Munro. 1997. Software Review, January 15, 1997- DecideRight. In *The Forum*, the newsletter of the International Association of Business Forecasting [http://www.loyola.edu/iabf/decide.htm]

2. Goodwin, P. and G. Wright. 1998. Decision analysis for management judgement, 2nd Ed. John Wiley & Sons, England. pp.454.

3. Mineau, P. A. Baril, B. T. Collins, J. Duffe, G. Joerman, R. Littik. 2001. Pesticide acute toxicity reference values. Rev. Environ. Contam. Toxicol. 170: 13-74.

Attachment D: Incident Data For Birds and Nontarget Mammals

The incidents reported here are summarized for each rodenticide from incident reports in the EPA/OPP Environmental Fate and Effect Division's Ecological Incidents Information System. Unless otherwise noted, an incident is included here only if confirmation of exposure is reported. For the anticoagulants, detection of residue in the liver is the criterion of exposure unless otherwise stated. Hemorrhaging and other signs of toxicosis also generally are included in incident reports, but details are not tabulated here (see Stone et al. 1999, 2003; Hosea 2000). For the non-anticoagulants, detection of bait in the stomach or crop contents are typical evidence of exposure. Most of the incidents are based on carcass recovery; however, as noted, 3 incidents involved mammals that were live-trapped and sacrificed. Reported residue levels are provided only as confirmation that animals were exposed to a rodenticide. There are no incident data for bromethalin and cholecalciferol.

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Owls						
Great horned owl	NY	Erie	4/04	1	0.026	the owl was observed on the ground in a lethargic state for 3 days before its death
Great horned owl	NY	Saratoga	2/02	1	0.44	"Little blood in heart (blood watery)"
Great horned owl	NY	Erie	12/01	1	0.82	
Great horned owl	NY	Delaware	10/01	1	0.84	
Great horned owl	NY	Rockland	9/01	1	0.24	
Great horned owl	NY	Ulster	4/01	1	0.49	
Great horned owl	CA	Los Angeles	2000	1	0.34	
Great horned owl	CA	Los Angeles	2000	1	0.05	also bromadiolone (0.8 ppm)

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Great horned owl	NY	Rensselaer	11/00	1	0.09	
Great horned owl	NY	Warren	10/00	1	0.15	also bromadiolone (0.32 ppm)
Great horned owl	NY	Suffolk	7/00	1	0.37	also bromadiolone (0.4 ppm)
Great horned owl	NY	Albany	10/99	1	0.14	
Great horned owl	CA	San Bernardino	10/99	1	0.35	also bromadiolone (0.065 ppm)
Great horned owl	NY	Washington	7/99	1	0.42	bird was a fledgling
Great horned owl	NY	Dutchess	2/99	1	0.64	brodifacoum also detected in an egg (0.008 ppm)
Great horned owl	NY	Suffolk	2/99	1	0.23	
Great horned owl	NY	Ontario	2/99	1	0.16	
Great horned owl	NY	Nassau	2/99	1	0.08	brodifacoum also detected in skeletal muscle (0.02 ppm); 4 dead rats found in owl's nest
Great horned owl	NY	Columbia	1/99	1	0.036	small mammal hair in stomach
Great horned owl	NY	Oswego	12/98	1	0.30	owl may have bled excessively from puncture wound between eyes and into the sinuses, possibly caused by its prey (partially-eaten muskrat carcass found nearby)
Great horned owl	NY	Albany	12/98	1	0.08	also bromadiolone (0.27 ppm); "The owl died from hemorrhaging of minor wounds inflicted by prey";

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Great horned owl	CA	Contra Costa	8/98	1	0.04	also diphacinone (0.6 ppm)
Great horned owl	NY	Niagara	7/98	1	0.03	also bromadiolone (0.77 ppm) and warfarin (0.73 ppm)
Great horned owl	NY	Rensselaer	7/98	1	0.12	a dead rat found nearby owl
Great horned owl	NY	Saratoga	5/98	1	0.06	also bromadiolone (0.24 ppm)
Great horned owl	GA	White	2/98	2	0.099 0.23	
Great horned owl	NY	Dutchess	6/97	1	0.22	
Great horned owl	NY	Genesee	4/97	1	0.09	
Great horned owl	NY	Greene	2/97	1	0.08	
Great horned owl	NY	Monroe	6/96	1	0.35	vole remains in stomach; small laceration on foot
Great horned owl	NY	Chenango	2/96	1	0.36	
Great horned owl	NY	Suffolk	8/95	1	0.53	also bromadiolone (0.14 ppm)
Great horned owl	CA	San Joaquin	1995	1	0.015	
Great horned owl	NY	Albany	12/94	1	0.1	
Great horned owl	NY	Orleans	11/94	1	0.73	bled from punctures on feet
Great horned owl	NY	Erie	10/94	1	0.41	
Great horned owl	NY	Albany	6/94	1	0.64	blood on feet from hole on left foot; brodifacoum bait applied nearby
Great horned owl	NY	Niagara	3/94	1	0.53	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Great horned owl	NY	Suffolk	10/89	1	0.2	
Great horned owl	NY	Putnam	3/89	1	0.01	
Long-eared owl	NY	Bronx	3/99	1	0.30	
Eastern screech-owl	NY	Suffolk	2/03	1	0.30	unidentified mammal hair and bones in the stomach
Eastern screech-owl	NY	Niagara	9/02	1	0.65	
Eastern screech-owl	NY	New York	1/02	1	0.91	
Eastern screech-owl	NY	Albany	2/00	1	0.16	
Eastern screech-owl	NY	Schenectady	10/99	1	0.16	
Eastern screech-owl	NY	Erie	10/97	1	0.8	
Eastern screech-owl	NY	Suffolk	2/97	1	0.34	
Barn owl	GA	Dawson	11/03	1	0.035	a red-tailed hawk also died, and vitamin K was administered to 2 great horned owls that showed signs of poisoning
Barn owl	CA	Sacramento	11/02	1	0.03	brodifacoum also detected in the ventriculus (4.90 ppb), along with mammal hairs, and in a blood sample taken from the thoracic cavity and ventriculus lining

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Barn owl	CA	San Bernardino	10/99	3	0.35	
					0.21	also bromadiolone (0.38 ppm)
					0.07	also bromadiolone (0.31 ppm)
Barn owl	GA	Madison	11/95	2	0.85	
					0.75	
Barred owl	NY	Albany	11/01	1	0.04	
Northern spotted owl	WA	Chelan	4/91	1	0.1	NWHC[b] database (case 10128)
Northern spotted owl	WA	Kittitas	7/95	1	0.05	NWHC[b] database (case 13799)
Diurnal Birds of Prey						
Golden eagle	CA	Ventura	2000	3	0.026	the 3 eagles were live-trapped for relocation but died in captivity
					0.01	
					0.004	
Golden eagle	CA	Alameda	11/99	1	0.01	
Golden eagle	CA	Contra Costa	11/99	1	trace	
Golden eagle	CA	Stanislaus	7/99	1	0.02	
Golden eagle	CA	Contra Costa	3/99	1	0.04	
Golden eagle	CA	Alameda	2/99	1	0.04	
Golden eagle	NY	Washington	12/97	1	0.016	
Golden eagle	CA	Alameda	11/97	1	0.08	
Golden eagle	CA	Santa Clara	5/97	1	trace	
Golden eagle	CA	San Benito	12/96	1	0.13	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Golden eagle	NY	Monroe	4/96	1	0.03	tissue analyzed 7 months after death
Bald eagle	WI	Sawyer	10/98	1	detected	residue level reported as "moderate"
Bald eagle	ID	Boise	1/86	1	38	reported by the NWHC[b] (case 6372)
Red-tailed hawk	NY	Schenectady	3/04	1	0.50	probable bite injury on left foot likely source of blood on belly plumage
Red-tailed hawk	GA	Dawson	11/03	1	0.08	residue from unspecified fresh tissue
Red-tailed hawk	NY	Suffolk	3/02	1	0.57	
Red-tailed hawk	NY	New York	3/02	1	0.4	
Red-tailed hawk	NY	Albany	3/01	1	0.03	bled severely from foot lacerations probably inflicted by prey
Red-tailed hawk	WI	LaCrosse	2/01	1	0.02	
Red-tailed hawk	WI	Dane	1/01	1	0.04	unidentified meat/muscle in crop
Red-tailed hawk	WI	LaCrosse	1/01	1	0.11	
Red-tailed hawk	WI	Outagamie	1/01	2	0.008	6 other hawks found alive but ill
Red-tailed hawk	WI	Iowa	1/01	1	0.04	
Red-tailed hawk	CA	San Luis Obispo	1/01	1	0.015	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Red-tailed hawk	AL	Morgan	1/01	4	0.01	8 red-tailed hawks and 24 undidentified hawks reported in this incident in the NWHC[b] database (case 13799)
Red-tailed hawk	WI	Buffalo	12/00	1	0.014	rodent hair, meat, bones in crop
Red-tailed hawk	NY	Rockland	12/00	1	0.32	
Red-tailed hawk	CA	San Joaquin	12/00	1	0.12	
Red-tailed hawk	WI	Dane	8/00	1	0.009	
Red-tailed hawk	WI	Adams	7/00	1	0.003	
Red-tailed hawk	WI	Columbia	5/00	1	0.02	
Red-tailed hawk	NY	Rensselaer	4/00	1	0.94	
Red-tailed hawk	NY	New York	3/00	1	0.24	small mammal hair and bone in stomach
Red-tailed hawk	NY	Westchester	3/00	1	0.377	
Red-tailed hawk	NY	Westchester	3/00	1	0.08	
Red-tailed hawk	WI	Manitowoc	3/00	1	0.03	
Red-tailed hawk	WI	Columbia	2/00	1	detected	residue level not reported
Red-tailed hawk	WI	Vernon	1/00	1	detected	residue level not reported
Red-tailed hawk	WI	Dane	1/00	1	detected	residue level not reported
Red-tailed hawk	NY	Rensselaer	6/99	1	0.69	
Red-tailed hawk	NY	Albany	4/99	1	0.32	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Red-tailed hawk	CA	Stanislaus	3/99	1	0.01	
Red-tailed hawk	NY	Nassau	3/99	1	1.28	
Red-tailed hawk	NY	Suffolk	2/99	1	0.80	this hawk apparently "bled out" through a minor leg wound possibly inflicted by its prey
Red-tailed hawk	NY	New York	1/99	1	0.23	
Red-tailed hawk	NY	Suffolk	1/99	1	0.13	
Red-tailed hawk	NY	Saratoga	1/99	1	0.16	severe blood loss may have been from minor bites on feet
Red-tailed hawk	NY	Albany	10/98	1	0.04	
Red-tailed hawk	NY	Nassau	1/98	1	0.56	
Red-tailed hawk	NY	Suffolk	10/96	1	0.5	mouse parts in GI tract
Red-tailed hawk	NY	Onondaga	6/96	1	0.65	small mammal fur in stomach
Red-tailed hawk	NY	Suffolk	12/95	1	1.6	blood stains on right foot and belly; rodenticide applied nearby
Red-tailed hawk	NY	Nassau	3/95	1	0.76	bled from foot punctures "probably inflicted by prey"
Red-tailed hawk	NY	Richmond	1/95	1	0.43	
Red-tailed hawk	NY	Westchester	12/94	1	0.23	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Red-tailed hawk	NY	Westchester	11/94	1	0.46	"The bird seemed to have exsanguinated through a minor toe wounds"
Red-shouldered hawk	NY	Westchester	4/02	1	0.23	
Red-shouldered hawk	CA	Stanislaus	3/99	2	0.15	
					0.01	also bromadiolone (0.28 ppm)
Cooper's hawk	NY	Dutchess	9/03	1	0.28	
Cooper's hawk	NY	Rensselaer	2/02	1	0.37	
Cooper's hawk	NY	Schenectady	2/01	1	0.18	
Cooper's hawk	NY	Albany	9/00	1	0.21	
Cooper's hawk	CA	Los Angeles	2000	1	0.03	
Cooper's hawk	WI	Manitowoc	3/00	1	0.03	
Sharp-shinned hawk	NY	Steuben	1/02	1	0.023	
Sharp-shinned hawk	NY	Schenectady	1/00	1	0.17	
Black vulture	NY	Westchester	4/02	1	0.13	
Turkey vulture	NY	Ulster	3/01	1	0.26	
Perching Birds						
Raven	NY	Rensselaer	4/96	1	1.04	
American crow	NY	Albany	1/02	1	1.73	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
American crow	NY	Oneida	10/01	1	1.9	
American crow	NY	Chautaugun	10/01	1	0.07	
American crow	NY	Erie	9/01	1	0.70	
American crow	NY	Oneida	9/01	1	1.5	
American crow	NY	Erie	7/01	1	0.52	
American crow	NY	Erie	6/01	1	0.35	
American crow	NY	Erie	5/01	1	1.3	
American crow	NY	Albany	3/01	1	0.45	
American crow	NY	Albany	2/01	1	0.4	
American crow	NY	Onondaga	8/00	1	0.08	
American crow	NY	Suffolk	6/00	1	1.0	
American crow	NY	Westchester	4/00	1	1.2	
Crow	NY	Dutchess	10/99	1	1.67	
Crow	NY	Westchester	9/98	2	0.14	pooled sample from both birds
Crow	CT	Norwalk	1/97	1	1.34	gizzard contained blue-green granular material believed to be bait
Other Birds						
Geese	VA	Fauquier	10/92	2	not reported	VA Dept. Game and Inland Fisheries attributed deaths to brodifacoum; no residue values provided

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Rock dove	CA	Ventura	5/03	1	0.01	also diphacinone (0.9 ppm)
Denver Zoo:	CO		11/86-1/87	10		liver residues were determined at the Denver Federal Center; deaths coincided with bait application and a massive mouse die-off
Plover					0.8	
Sissa					0.5	
Franklin’s gull					1.5-1.6	
Laughing gull					1.6	
National Zoo:	VA		4/84	~12	confirmed	birds apparently died after eating crickets that had consumed bait; according to EPA memo, "residues in birds were confirmed by ICI, the registrant"; memo also notes that a similar incident occurred at the Philadelphia Zoo 3 years earlier
Avocet						
Ant pitta						
Golden plover						
Honey creeper						
Finch						
Thrush						
Warbler						
Crake						
Carnivores						
Coyote	CA	Los Angeles	2000	1	0.08	also bromadiolone (0.44 ppm)
Coyote	NY	Warren	5/99	1	0.93	
Coyote	CA	Santa Clara	2/99	5	0.47	also bromadiolone (0.46 ppm)
					0.36	also chlorophacinone (trace)
					0.30	also bromadiolone (0.07 ppm)
					0.23	also bromadiolone (0.09 ppm)
					0.33	all 5 coyotes were live-trapped and sacrificed

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Coyote	CA	Santa Clara	1999	1	0.07	
Coyote	CA	Santa Clara	1999	1	0.03	
Coyote	CA	Santa Clara	1999	1	0.28	
Coyote	CA	Santa Clara	1999	1	0.06	
Coyote	CA	San Mateo	1998	1	0.08	
Coyote	CA	Ventura	1998	1	0.04	
Coyote	CA	Los Angeles	1998	1	0.08	also chlorophacinone (0.43 ppm) and diphacinone (0.08 ppm); coyote live-trapped and sacrificed
Coyote	CA	Orange	1998	2	0.5 0.66	also bromadiolone (0.22 ppm); coyotes live-trapped and sacrificed
Coyote	CA	Los Angeles	12/97	1	0.28	also detected in blood (0.019 ppm)
Coyote	CA	Ventura	10/97	1	0.083	also diphacinone (1.3 ppm)
Coyote	CA	Los Angeles	8/97	2	0.054 trace	
Coyote	CA	Ventura	8/97	1	trace	
San Joaquin Kit Fox	CA	Kern	8/03	1	11.0	
San Joaquin Kit Fox	CA	Kern	2002	1	0.706	
San Joaquin Kit Fox	CA	Kern	2002	1	0.381	
San Joaquin Kit Fox	CA	Kern	2002	1	0.373	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
San Joaquin Kit Fox	CA	Kern	2002	1	0.296	
San Joaquin Kit Fox	CA	Kern	2002	1	0.161	
San Joaquin Kit Fox	CA	Kern	2002	1	0.132	
San Joaquin Kit Fox	CA	Kern	2002	1	0.191	also pival[c] (6.93 ppm) and coumatetralyl[d] (0.368 ppm)
San Joaquin Kit Fox	CA	Kern	2002	1	0.122	also coumatetralyl[d] (1.42 ppm)
San Joaquin Kit Fox	CA	Kern	2002	1	0.019	coumatetralyl[d] (0.4 ppm)
San Joaquin Kit Fox	CA	Kern	2002	1	0.091	coumatetralyl[d] (1.1 ppm)
San Joaquin Kit Fox	CA	Kern	2002	1	0.009	coumatetralyl[d] (0.134 ppm)
San Joaquin Kit Fox	CA	Kern	2002	1	0.008	
San Joaquin Kit Fox	CA	Kern	2002	1	0.007	
San Joaquin Kit Fox	CA	Kern	2002	1	trace	
San Joaquin Kit Fox	CA	Tulare	2001	1	0.042	
San Joaquin Kit Fox	CA	Kern	2001	1	0.18	
San Joaquin Kit Fox	CA	Kern	2001	1	0.075	
San Joaquin Kit Fox	CA	Kings	2001	1	trace	
San Joaquin Kit Fox	CA	Kern	2000	1	1.0	
San Joaquin Kit Fox	CA	Kern	2000	1	0.11	
San Joaquin Kit Fox	CA	Kern	2000	1	0.1	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
San Joaquin Kit Fox	CA	Kern	1/00	1	0.13	also bromadiolone (0.14 ppm); roadside carcass
San Joaquin Kit Fox	CA	Kern	12/99	1	0.67	roadside carcass
San Joaquin Kit Fox	CA	Kern	11/99	1	0.22	animal hit by car and died
San Joaquin Kit Fox	CA	Kern	8/99	1	0.47	also bromadiolone (0.72 ppm)
San Joaquin Kit Fox	CA	Kern	9/99	1	0.07	also chlorophacinone (0.27 ppm)
Red fox	NY	Suffolk	3/96	2	4.01 1.32	also detected in alimentary canal contents (0.34 ppm), which contained deer hair; 4 dead deer, not analyzed, also were found
Red fox	CA	Monterey	1999	1	0.04	
Red fox	CA	Fresno	8/97	2	0.05	rodent bones and hair, feathers, and grain present in stomach
Gray fox	NY	Albany	8/99	1	0.35	
Gray fox	NY	Delaware	3/98	1	0.02	small mammal skin and hair in stomach
Gray fox	CA	Los Angeles	1998	1	0.03	
Bobcat	CA	Los Angeles	2/01	1	0.024	
Bobcat	CA	Ventura	9/99	1	0.07	also bromadiolone (0.11 ppm)
Bobcat	CA	Riverside	6/99	1	0.018	
Bobcat	CA	Ventura	12/97	1	0.049	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Mountain lion	CA	Riverside	4/97	1	0.52	
Raccoon	NY	New York	5/00	1	0.14	
Raccoon	CA	Los Angeles	1998	1	0.082	also bromadiolone (1.1 ppm) and diphacinone (0.13 ppm); raccoon live-trapped and sacrificed
Raccoon	CA	Orange	1998	1	0.011	also bromadiolone (0.41 ppm); raccoon live-trapped and sacrificed
Raccoon	NY	Albany	3/97	1	0.32	
Raccoon	NY	Suffolk	3/96	1	1.0	blue-green granular material, probably bait, in stomach
Raccoon	NY	Nassau	9/92	3	5.3 4.6 3.1	
Raccoon	NY	Niagara	6/92	1	1.8	detected in stomach contents; dyed bait also present in stomach
Long-tailed weasel	NY	Rensselaer	1/00	1	0.07	
Striped skunk	NY	Albany	5/99	1	1.05	
Striped skunk	NY	Delaware	3/98	1	0.3	small mammal fur in stomach
Marsupials						
Opossum	NY	Albany	12/98	1	0.24	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Opossum	NY	Albany	4/97	1	0.18	
Ungulates						
White-tailed deer	NY	Suffolk	12/97	1	0.16	
White-tailed deer	NY	Suffolk	4/96	1	0.12	
White-tailed deer	NY	Suffolk	5/96	1	0.41	
White-tailed deer	NY	Suffolk	9/95	1	0.37	also coumatetralyl (0.5 ppm)
White-tailed deer	NY	Suffolk	10/94	1	0.38	
Rodents						
Gray squirrel	NY	Albany	2/02	1	0.82	third dead squirrel found in 2 weeks
Gray squirrel	NY	Dutchess	10/01	3	5.5 1.03	
Gray squirrel	NY	Livingston	8/01	1	3.45	second squirrel found dead in a week
Gray squirrel	NY	Schenectady	8/01	1	2.64	
Gray squirrel	NY	Rockland	6/01	1	0.35	
Gray squirrel	NY	New York	2/01	1	0.3	
Gray squirrel	NY	Albany	4/00	2	8.3 4.1	
Gray squirrel	NY	Suffolk	12/99	2	0.70 0.25	

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Gray squirrel	NY	Albany	11/99	1	2.1	
Gray squirrel	NY	Rensselaer	8/99	1	2.4	
Gray squirrel	NY	Albany	7/99	1	0.31	
Gray squirrel	NY	Westchester	5/99	1	6.3	
Gray squirrel	NY	Westchester	5/99	3	2.4	
Gray squirrel	NY	Albany	5/99	1	0.23	
Gray squirrel	NY	New York	5/99	1	3.12	
Gray squirrel	NY	Westchester	4/99	3	6.44 6.93 6.9	also detected in stomach (10.3 ppm)
Gray squirrel	NY	Oneida	9/98	5	detected	reportedly detected at "significant" levels
Gray squirrel	NY	Nassau	3/97	1	0.88	the squirrel was found dead on 3/97 but not necropsied until 1/99
Gray squirrel	WI	Calumet	4-5/97	3	detected	residue level reported as "significant"
Gray squirrel	NY	Albany	12/96	1	1.39	
Gray squirrel	WI	Calumet	9/96	2	detected	residue level not reported
Gray squirrel	WI	Calumet	8/95	1	1.8	~30 other dead squirrels found, but not analyzed, between 2-8/95 in a neighborhood in Appleton, WI

Brodifacoum[a]

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Gray squirrel	NY	Albany	9/93	1	25.8	detected in colon contents; dyed bait also present in alimentary canal
Gray squirrel	NY	Albany	8/93	1	0.53	also chlorophacinone (0.62 ppm)
Gray squirrel	NY	Monroe	6/93	3	5.1	pooled sample
Gray squirrel	VA	Henrico	6/93	4	detected	residue level reported as "significant"; a cat also was treated for poisoning
Gray squirrel	NY	Monroe	7/90	1	4.1	
Gray squirrel	NY	Westchester	6/90	1	0.7	
Fox squirrel	CA	Sacramento	5/99	8	3.1	apparent deliberate misuse
Chipmunk	WI	Oneida	9/98	3	detected	present at "significant levels" in a pooled sample
Chipmunk	NY	Albany	6/92	1	3.8	

[a] two additional incidents were submitted by Syngenta under 6(a)(2) aggregate reporting; the species and number of individuals involved were not reported

[b] National Wildlife Health Center, Madison, WI; incident information from the Center's diagnostic file of individual birds submitted for examination or from their epizootic database (K. Converse, pers comm.)

[c] pival, a first-generation anticoagulant, is no longer registered in the U.S. but might have been used under existing stocks provisions

[d] coumatetralyl, a second-generation anticoagulant, is not registered for use in the U.S.

Difethialone

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Carnivores						
Bobcat	CA	Los Angeles	1999	1	trace	

Bromadiolone

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Owls						
Great horned owl	NY	Warren	10/00	1	0.32	also brodifacoum (0.15 ppm)
Great horned owl	NY	Suffolk	7/00	1	0.4	also brodifacoum (0.37 ppm)
Great horned owl	NY	Albany	7/00	1	detected	
Great horned owl	CA	Los Angeles	2000	1	0.8	also brodifacoum (0.05 ppm)
Great horned owl	CA	San Bernardino	10/99	1	0.065	also brodifacoum (0.35 ppm)
Great horned owl	NY	Albany	12/98	1	0.27	also brodifacoum (0.08 ppm); "The owl died from hemorrhaging of minor wounds inflicted by prey"
Great horned owl	NY	Niagara	7/98	1	0.77	also warfarin (0.73 ppm) and brodifacoum (0.03 ppm)
Great horned owl	NY	Saratoga	5/98	1	0.24	also brodifacoum (0.06 ppm)
Great horned owl	NY	Suffolk	8/95	1	0.14	also brodifacoum (0.53 ppm)
Eastern screech-owl	NY	Cattaragus	1/00	1	4.29	
Eastern screech-owl	NY	Suffolk	3/99	1	0.05	
Northern saw-whet owl	NY	Cattaraugus	3/00	1	0.43	

Bromadiolone

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Barn owl	CA	San Bernardino	10/99	3	0.38 0.31 0.38	also brodifacoum (0.21 ppm) also brodifacoum (0.07 ppm) A total of 29 owls, 6 hawks, and 1 egret were found dead
Diurnal Birds of Prey						
Red-shouldered hawk	CA	Stanislaus	1999	1	0.28	also brodifacoum (0.01 ppm)
Red-tailed hawk	NY	not reported	10/98	1	0.08	
Cooper's hawk	NY	Erie	12/00	1	0.6	
Cooper's hawk	NY	Greene	2/99	1	0.24	several puncture wounds, coated with dried blood, on foot
American kestrel	CA	Yolo	1998	1	trace	detected in a nestling
Herons						
Great blue heron	NY	New York	1/99	1	0.1	
Perching Birds						
Fish crow	NY	Richmond	4/00	1	2.1	
Doves						
Mourning dove	NY	New York	10/99	1	0.42	

Bromadiolone

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Carnivores						
San Joaquin Kit Fox	CA	Kern	1/00	1	0.14	also brodifacoum (0.13 ppm)
San Joaquin Kit Fox	CA	Kern	1999	1	0.72	also brodifacoum (0.47 ppm)
Coyote	CA	Los Angeles	2000	1	0.44	also brodifacoum (0.08 ppm)
Coyote	CA	Santa Clara	1999	3	0.46 0.09 0.07	also brodifacoum (0.47 ppm) also brodifacoum (0.23 ppm) also brodifacoum (0.30 ppm)
Coyote	CA	Orange	1998	1	0.22	also brodifacoum (0.66 ppm); coyote live-trapped and sacrificed
Bobcat	CA	Ventura	1999	1	0.11	also brodifacoum (0.07 ppm)
Raccoon	CA	Los Angeles	1998	1	1.1	also brodifacoum (0.082 ppm) and diphacinone (0.13 ppm); raccoon live-trapped and sacrificed
Raccoon	CA	Orange	1998	1	0.41	also brodifacoum (0.011 ppm); raccoon live-trapped and sacrificed
Striped skunk	NY	Westchester	4/96	3	0.2 0.29 0.08	
Marsupials						
Opossum	NY	Albany	11/96	1	0.8	

Bromadiolone

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Rodents						
Gray squirrel	NY	New York	2/01	1	0.3	
Gray squirrel	NY	Suffolk	6/00	1	0.003	
Gray squirrel	NY		6/00	1	2.92	also detected (0.021 ppm) in stomach contents
Gray squirrel	NY	New York	4/00	3	8.84 3.14 2.46	
Gray squirrel	NY	Erie	11/99	3	2.88 1.43 1.01	all 3 squirrels had undergone considerable autolysis
Gray squirrel	NY	New York	2/99	1	0.05	
Gray squirrel	NY	Onondaga	9/98	1	0.12	
Gray squirrel	VA	Richmond	6/98	2	4.94	pooled sample from 2 of 8 squirrels found dead; also diphacinone (3.41 ppm); several unidentified birds also found dead

Chlorophacinone

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Diurnal Birds of Prey						
Red-tailed hawk	NY	New York	7/99	1	0.18	
Gallinaceous Birds						
Turkey (wild)	KS	Cheyenne	4/02	2	0.69 0.40	bait present in gastrointestinal tract
Turkey (wild)	CA	Nevada	12/94	3	0	residues confirmed in gut contents; also detected in blood (5.5 ppm)
Carnivores						
Coyote	CA	Santa Clara	2/99	1	trace	also brodifacoum (0.36 ppm); the animal was live-trapped and sacrificed
Coyote	CA	Los Angeles	7/98	1	0.43	also brodifacoum (0.08 ppm) and diphacinone (0.081 ppm); the animal was live-trapped and sacrificed
Coyote	CA	Los Angeles	9/97	1	1.2	
San Joaquin kit fox	CA	Kern	9/99	1	0.27	also brodifacoum (0.07 ppm)
San Joaquin kit fox	CA	San Luis Obispo	8/90	4	detected	residue levels not reported

Chlorophacinone

Order/ species	Stat e	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Bobcat	CA	Marin	7/95	1	0.4	bobcat found dead 1 day after seen feeding on a dead owl; a rodent carcass was recovered in the crop of the owl
Rodents						
Gray squirrel	NY	New York	2/99	1	0.44	
Gray squirrel	NY	New York	1/99	1	0.47	
Gray squirrel	NY	New York	1/99	1	0.29	
Gray squirrel	NY	Albany	8/93	1	0.62	also brodifacoum (0.53 ppm)

Diphacinone

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Owls						
Barred owl	NY	Schenectady	11/99	1	0.62	immediate cause of death apparently was blunt trauma, possibly impact by an automobile
Great horned owl	CA	Contra Costa	8/98	1	0.6	also brodifacoum (0.04 ppm)
Snowy owl	NY	Dutchess	11/93	1	0.26	
Diurnal Birds of Prey						
Red-tailed hawk	NY	Nassau	6/99	1	0.34	
Turkey vulture	CA	Alameda	7/97	1	0.4	
Other Birds						
Rock dove	CA	Ventura	5/03	1	0.9	also brodifacoum (0.01 ppm)
Carnivores						
San Joaquin kit fox	CA	Kern	6/87	1	0.18	anticoagulant baits had been applied in the area for ground squirrel control
Coyote	CA	Ventura	10/97	1	1.3	also in thoracic-cavity blood (0.1 ppm) and stomach contents (0.16 ppm); also brodifacoum (0.083 ppm)

Diphacinone

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Coyote	CA	Los Angeles	1998	1	0.081	also chlorophacinone (0.43 ppm) and brodifacoum (0.08 ppm); the animal was live-trapped and sacrificed
Coyote	CA	Los Angeles	9/97	1	0.043	
Mountain lion	CA		11/86	1	see comment	45 ppm detected in blood
Raccoon	CA	Los Angeles	1998	1	0.13	also bromadiolone (1.1 ppm) and brodifacoum (0.082 ppm); the animal was live-trapped and sacrificed
Raccoon	CA		11/86	1	see comment	44 ppm detected in "blood and liver" sample
Ungulates						
White-tailed deer	NY	Suffolk	12/96	1	0.2	maggots in carcass suggest the deer had probably been dead for several weeks prior to analysis
White-tailed deer	NY	Suffolk	10/96	1	0.93	
Rodents						
Gray squirrel	NY	Albany	3/00	1	1.02	

Diphacinone

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Gray squirrel	VA	Richmond	6/98	2	3.41	pooled sample; also bromadiolone (4.94 ppm); 6 other squirrels and several unidentified birds also found dead
Gray squirrel	NY	Suffolk	4/97	1	2.0	
Heermann’s kangaroo rat	CA	Merced	4/94	1	3.5	
Rabbits						
Cottontail rabbit	CA	Kern	8/89	12	not analyzed	reported by CA Dept. Fish and Game as "circumstantially indicated, but not conclusive" - dead rabbits found in area where diphacinone was applied; bleeding and hemorrhaging suggested anticoagulant poisoning

Warfarin

Order/ species	State	County	Date	No. animals analyzed	Liver residue (ppm)	Comments
Owls						
Great-horned owl	NY	Niagra	7/98	1	0.73	also bromadiolone (0.77 ppm) and brodifacoum (0.03 ppm)
Diurnal Birds of Prey						
Bald eagle	NY	Orleans	4/95	1	1.45	
Peregrine falcon	NJ	Sea Isle City	10/86	1	1.48	small bird parts were observed in the gizzard
Rodents						
Gray squirrel	NY	Niagara	9/81	1	0.23	

Zinc Phosphide

Order/ species	Stat e	County	Date	No. animals examined	Comments
Gallinaceous Birds					
Turkey (wild)	NY	Wayne	2/00	2	detected in crop contents
Turkey (wild)	MI	Montcalm	12/97	3	detected in crop contents
Turkey (wild)	NY	Wayne	11/95	1	detected in crop contents
Turkey (wild)	WI	not reported	3/91	2	turkey found dead after bait applied in an orchard
Turkey (wild)	MI	Manistee	12/87	4	27 ppm
Turkey (wild)	MI	Leelanau	11/87	1	170 ppm in gizzard contents
Turkey (wild)	MI	Leelanau	4/87	1	28 ppm in gizzard contents
Turkey (wild)	MI	Missaukee	3/87	1	220 ppm in gizzard contents
Turkey (wild)	MI	Benzie	12/86	9	430 ppm in gizzard contents
Turkey (wild)	MI	Wexford	11/86	4	330 ppm in gizzard contents
Turkey (wild)	MI	Grand Traverse	11/86	4	confirmed by MI Dept. of Agric. lab. analysis
Waterfowl					
Canada goose	NY	Niagra	12/01	4-5	15 geese found dead, with phosphine odor present; 3 of 4 geese analyzed with Draeger apparatus tested positive for phosphine gas
Canada goose	NY	Ulster	12/96	4	phosphine gas detected in ingesta
Canada goose	UT	Summit	4/94	1	information obtained from epizootic database, National Wildlife Health Center, Madison, WI

Zinc Phosphide

Order/ species	Stat e	County	Date	No. animals examined	Comments
Canada goose	CT	Fairfield	3/92	9	information obtained from epizootic database, National Wildlife Health Center, Madison, WI
Canada goose	MI	Grand Traverse	11/86	1	20 ppm residue in gizzard contents
Canada goose	MI	Oakland	12/82	30	confirmed by MI Dept. of Agric. lab. analysis
Canada goose	CA	Siskiyou	10/63	105	Keith and O'Neill[b]
White-fronted goose	CA	Siskiyou	10/63	325	Keith and O'Neill[b]
Snow goose	CA	Siskiyou	10/63	25	Keith and O'Neill[b]
White-fronted and Snow geese	CA	Siskiyou	4/84	~40	information obtained from epizootic database, National Wildlife Health Center, Madison, WI
Mallard	UT	Summit	10/93-4/94	29	information obtained from epizootic database, National Wildlife Health Center, Madison, WI
Carnivores					
Red fox	MI	Grand Traverse	6/87	2	"secondary poisoning from eating mice that had consumed Zn_phosphide treated grain"[a]
Other Mammals					
Eastern cottontail	VA	Augusta	1/04	1	>40 ppm in fresh tissues: ZP pellets had been applied in an orchard
Gray squirrel	MI	Calhoun	6/83	10	information obtained from epizootic database, National Wildlife Health Center, Madison, WI

[a] reported in Johnson and Fagerstone (1992) and Hegdal and Gatz (1977)

Attachment E. USFWS Jeopardy Determinations for Effects of 8 Rodenticides on Threatened and Endangered Species.

In response to a formal consultation requested by EPA (1991b) under Section 7 of the Endangered Species Act, the United States Fish and Wildlife Service issued a Biological Opinion on *Effects of 16 Vertebrate Control Agents On Threatened and Endangered Species* in March of 1993 (USFWS 1993). The Biological Opinion included jeopardy determinations for species potentially exposed (primary or secondary exposure) to brodifacoum, bromadiolone, chlorophacinone, diphacinone, warfarin, bromethalin, zinc phosphide, and cholecalciferol. For each species addressed in the Biological Opinion, the Service determined either that use of the rodenticide "is likely to jeopardize" or "is not likely to jeopardize" the continued existence of the species. For the likely to jeopardize determinations the Service provided "reasonable and prudent alternatives" that preclude jeopardy but still allow use of the rodenticide. These alternatives represent the Service's best professional judgement of the measures necessary to provide the appropriate level of protection to the species. The Service also provided "incidental take" statements and "reasonable and prudent measures" to minimize take. Difethialone, first registered in 1995, is not addressed in this or any subsequent Biological Opinion, but EPA believes the jeopardy determinations for brodifacoum also would be applicable to difethialone. The Service's determinations for each rodenticide are tabulated below. Only the common names of the species are presented in the table for each rodenticide, but scientific names are listed in a final table. Species not included in the tables were presumed by the Service to not be affected by the rodenticide of concern or to have no chance for exposure.

Brodifacoum

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which brodifacoum "is likely to jeopardize" their continued existence:	
Alabama beach mouse Choctawhatchee beach mouse Perdido Key beach mouse Anastasia Island beach mouse Southeastern beach mouse Morro Bay kangaroo rat Salt marsh harvest mouse Fresno kangaroo rat	Prohibit use within 100 yards of these species' occupied habitat
Carolina northern flying squirrel	Prohibit outdoor use within this species' occupied habitat
Florida salt marsh vole	Prohibit use within 100 yards of the landward edge of this species' habitat in Levy County, Florida
Audubon's crested caracara	Prohibit use within this species' occupied habitat
San Clemente loggerhead shrike	Prohibit use on San Clemente Island, California

Brodifacoum

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which brodifacoum "is not likely to jeopardize" their continued existence:	
Giant kangaroo rat Stephen's kangaroo rat Tipton kangaroo rat Point Arena mountain beaver	Incidental take can be minimized by prohibiting outdoor use within 100 yards of these species' occupied habitat
Louisiana black bear	Incidental take can be minimized by prohibiting use within occupied habitat
San Joaquin kit fox	Incidental take can be minimized by requiring that outdoor applications be made in tamper-resistant bait boxes placed in areas not accessible to wildlife
Hawaiian hawk	Incidental take can be minimized by prohibiting use within 100 yards of this species' occupied habitat
Eastern indigo snake	Incidental take can be minimized by conducting laboratory studies using surrogate snake species to obtain toxicity data on the chemical's secondary poisoning hazard to snakes

Bromadiolone

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which bromadiolone "is likely to jeopardize" their continued existence:	
Alabama beach mouse Choctawhatchee beach mouse Perdido Key beach mouse Anastasia Island beach mouse Southeastern beach mouse Morro Bay kangaroo rat Salt marsh harvest mouse	Prohibit use within 100 yards of these species' occupied habitat
Species for which bromadiolone "is not likely to jeopardize" their continued existence:	
Fresno kangaroo rat Stephen's kangaroo rat Tipton kangaroo rat Point Arena mountain beaver	Incidental take can be minimized by prohibiting outdoor use within 100 yards of these species' occupied habitat

Bromadiolone

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
San Joaquin kit fox	Incidental take can be minimized by requiring that outdoor applications be made in tamper-resistant bait boxes placed in areas not accessible to wildlife

Chlorophacinone

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which chlorophacinone "is likely to jeopardize" their continued existence:	
Alabama beach mouse Choctawhatchee beach mouse Perdido Key beach mouse Anastasia Island beach mouse Southeastern beach mouse Morro Bay kangaroo rat Stephen's kangaroo rat Amargosa vole Hualapai Mexican vole	Prohibit use within 100 yards of these species' occupied habitat
Salt marsh harvest mouse Tipton kangaroo rat Giant kangaroo rat Fresno kangaroo rat Point Arena mountain beaver	Prohibit outdoor use within 100 yards of these species' occupied habitat unless specific programs for chlorophacinone are approved by the Service and implemented
Carolina northern flying squirrel	Prohibit outdoor use within this species' occupied habitat
Florida salt marsh vole	Prohibit use within 100 yards of the landward edge of this species' habitat in Levy County, Florida
San Joaquin kit fox	Prohibit use within the kit fox range as determined by the Service, except for agricultural areas $\geq$1 mile from any kit fox habitat as determined by the California EPA in consultation with the Service, or areas where applicable surveys have been conducted and yielded negative results

Chlorophacinone

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Florida panther	Prohibit use within 20 miles of the boundary of any Federal and State lands (e.g., National Wildlife Refuge, National Park, State Park, etc.) and Indian Reservations that provide suitable panther habitat south of Charlotte, Glades and Martin counties, Florida; incidental take can be minimized by removing and properly disposing of any dead or incapacitated animal likely to have been poisoned within and including the area extending 5 miles from the edge of the prohibited use zone
Jaguarundi Ocelot	Prohibit use within 3 miles of occupied habitat; incidental take can be minimized by conducting surveys prior to use to determine if habitat is occupied
Audubon’s crested caracara	Prohibit use within this species’ occupied habitat
Species for which chlorophacinone "is not likely to jeopardize" their continued existence:	
Louisiana black bear	Incidental take can be minimized by prohibiting use within occupied habitat
Grizzly bear Gray wolf Utah prairie dog	None specified
Puerto Rican boa Virgin Island tree boa	Incidental take can be minimized by prohibiting use within the known occupied habitat
Eastern indigo snake	Incidental take can be minimized by conducting laboratory studies using surrogate snake species to obtain toxicity data on the chemical’s secondary poisoning hazard to snakes

Diphacinone

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which diphacinone "is likely to jeopardize" their continued existence:	
Alabama beach mouse Choctawhatchee beach mouse Perdido Key beach mouse Anastasia Island beach mouse Key Largo cotton mouse Key Largo woodrat Southeastern beach mouse Morro Bay kangaroo rat Stephen's kangaroo rat Silver rice rat Hualapai Mexican vole Utah prairiedog	Prohibit use within 100 yards of these species' occupied habitat
Salt marsh harvest mouse Tipton kangaroo rat Giant kangaroo rat Fresno kangaroo rat Point Arena mountain beaver	Prohibit outdoor use within 100 yards of these species' occupied habitat unless specific programs for diphacinone are approved by the Service and implemented
Carolina northern flying squirrel	Prohibit outdoor use within this species' occupied habitat
Florida salt marsh vole	Prohibit use within 100 yards of the landward edge of this species' habitat in Levy County, Florida
San Joaquin kit fox	Prohibit use within the kit fox range as determined by the Service, except for agricultural areas $\geq$1 mile from any kit fox habitat as determined by the California EPA in consultation with the Service, or areas where applicable surveys have been conducted and yielded negative results
Florida panther	Prohibit use within 20 miles of the boundary of any Federal and State lands (e.g., National Wildlife Refuge, National Park, State Park, etc.) and Indian Reservations that provide suitable panther habitat south of Charlotte, Glades and Martin counties, Florida; incidental take can be minimized by removing and properly disposing of any dead or incapacitated animal likely to have been poisoned within and including the area extending 5 miles from the edge of the prohibited use zone

Diphacinone

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Jaguarundi Ocelot	Prohibit use within 3 miles of occupied habitat; incidental take can be minimized by conducting surveys prior to use to determine if habitat is occupied
Gray wolf Grizzly bear	Prohibit use within the geographic range of this species until the Service has determined the species is not in the vicinity of the treatment site
Louisiana black bear	Prohibit use within the current known occupied habitat
Black-footed ferret	Prohibit use within 7 km (4.34 mi) from a prairie dog town, except for black-tailed prairie dog colonies <80 acres in size or white-tailed prairie dog colonies <200 acres in size, or urban situations, or colonies that have been surveyed in coordination with the Service and determined that ferrets are absent
Lower Keys rabbit	Prohibit use within 100 yards of this species' occupied habitat
Audubon's crested caracara	Prohibit use within this species' occupied habitat
Species for which diphacinone "is not likely to jeopardize" their continued existence:	
Delmarva fox squirrel	Incidental take can be minimized by placing bait in bait boxes small enough to exclude fox squirrels
Puerto Rican boa Virgin Island tree boa	Incidental take can be minimized by prohibiting use within the known occupied habitat
Eastern indigo snake	Incidental take can be minimized by conducting laboratory studies using surrogate snake species to obtain toxicity data on the chemical's secondary poisoning hazard to snakes

Warfarin

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which warfarin "is likely to jeopardize" their continued existence:	
Alabama beach mouse Choctawhatchee beach mouse Perdido Key beach mouse Anastasia Island beach mouse Southeastern beach mouse Morro Bay kangaroo rat Salt marsh harvest mouse Fresno kangaroo rat	Prohibit use within 100 yards of these species' occupied habitat
Carolina northern flying squirrel	Prohibit outdoor use within this species' occupied habitat
Florida salt marsh vole	Prohibit use within 100 yards of the landward edge of this species' habitat in Levy County, Florida
Species for which warfarin "is not likely to jeopardize" their continued existence:	
Giant kangaroo rat Stephen's kangaroo rat Tipton kangaroo rat Point Arena mountain beaver	Incidental take can be minimized by prohibiting outdoor use within 100 yards of these species' occupied habitat

Bromethalin

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which bromethalin "is likely to jeopardize" their continued existence:	
Alabama beach mouse Choctawhatchee beach mouse Perdido Key beach mouse Anastasia Island beach mouse Southeastern beach mouse Morro Bay kangaroo rat	Prohibit use within 100 yards of these species' occupied habitat
Salt marsh harvest mouse Fresno kangaroo rat	Prohibit use within 100 yards of these species' occupied habitat
Carolina northern flying squirrel	Prohibit outdoor use within this species' occupied habitat
Florida salt marsh vole	Prohibit use within 100 yards of the landward edge of this species' habitat in Levy County, Florida

Bromethalin

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which bromethalin "is not likely to jeopardize" their continued existence:	
Giant kangaroo rat Stephen's kangaroo rat Tipton kangaroo rat Point Arena mountain beaver	Incidental take can be minimized by prohibiting outdoor use within 100 yards of these species' occupied habitat

Zinc phosphide

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which zinc phosphide "is likely to jeopardize" their continued existence:	
Alabama beach mouse Choctawhatchee beach mouse Perdido Key beach mouse Anastasia Island beach mouse Southeastern beach mouse Morro Bay kangaroo rat Silver rice rat	Prohibit use within 100 yards of these species' occupied habitat
Fresno kangaroo rat Stephen's kangaroo rat Tipton kangaroo rat Giant kangaroo rat Salt marsh harvest mouse Point Arena mountain beaver	Prohibit outdoor use within 100 yards of occupied habitat unless a protection program has been approved by the Service and implemented
Carolina northern flying squirrel	Prohibit outdoor use within this species' occupied habitat
Florida salt marsh vole	Prohibit use within 100 yards of the landward edge of this species' habitat in Levy County, Florida
Black-footed ferret	Prohibit use within 7 km (4.34 mi) from a prairie dog town, except for black-tailed prairie dog colonies <80 acres in size or white-tailed prairie dog colonies <200 acres in size, or urban situations, or colonies that have been surveyed in coordination with the Service and determined that ferrets are absent
Hawaiian crow	Prohibit use within 100 yards of occupied habitat unless bait is placed in tamper-resistant bait boxes

Zinc phosphide

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Atwater’s prairie chicken	Prohibit use within 100 yards of occupied habitat unless bait is placed in tamper-resistant bait boxes
Hawaiian coot Hawaiian duck	Prohibit use within 100 yards of any water or wetland on or adjacent to any golf course or turf farm on the islands of Kauai, Oahu, and Maui unless bait is placed in tamper-resistant bait boxes
Nene (Hawaiian goose) Mariana crow	Prohibit use in occupied habitat unless bait is placed in tamper-resistant bait boxes
Mississippi sandhill crane Puerto Rican plain pigeon Yellow-shouldered blackbird	Outdoor baiting must use tamper-resistant bait boxes within occupied habitat
Species for which zinc phosphide "is not likely to jeopardize" their continued existence:	
Gray wolf Grizzly bear	Incidental take can be minimized by applying bait in tamper-resistant bait boxes, or contacting the local Service office to ensure that these species are not in the vicinity of the treatment site
Utah prairie dog	None specified
San Joaquin kit fox	Incidental take can be minimized by requiring that outdoor applications be made in tamper-resistant bait boxes placed in areas not accessible to wildlife
San Clemente sage sparrow	Incidental take can be minimized by prohibiting use in occupied habitat unless bait is placed in tamper-resistant bait boxes
Whooping crane	Incidental take can be minimized by ensuring that cranes have not wandered into the treatment area

Cholecalciferol

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Species for which cholecalciferol "is likely to jeopardize" their continued existence:	

Cholecalciferol

Species	Reasonable and Prudent Alternatives/ Reasonable and Prudent Measures
Alabama beach mouse Choctawhatchee beach mouse Perdido Key beach mouse Anastasia Island beach mouse Southeastern beach mouse Morro Bay kangaroo rat Salt marsh harvest mouse Fresno kangaroo rat	Prohibit use within 100 yards of these species' occupied habitat
Carolina northern flying squirrel	Prohibit outdoor use within this species' occupied habitat
Florida salt marsh vole	Prohibit use within 100 yards of the landward edge of this species' habitat in Levy County, Florida
Species for which cholecalciferol "is not likely to jeopardize" their continued existence:	
Giant kangaroo rat Stephen's kangaroo rat Tipton kangaroo rat Point Arena mountain beaver	Incidental take can be minimized by prohibiting outdoor use within 100 yards of these species' occupied habitat

Species addressed in the Biological Opinion[a]:

Mammals:

Alabama beach mouse (*Peromyscus polionotus amnobates*)

Amargosa vole (*Microtus californicus scirpensis*)

Anastasia Island beach mouse (*Peromyscus polionotus phasma*)

Black-footed ferret (*Mustela nigripes*)

Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*)

Choctawhatchee beach mouse (*Peromyscus polionotus allophrys*)

Delmarva fox squirrel (*Sciurus niger cinereus*)

Florida salt marsh vole (*Microtus pennsylvanicus dukecampbelli*)

Florida panther (*Puma (=Felis) concolor coryi*)

Fresno kangaroo rat (*Dipodomys nitratoides exilis*)

Giant kangaroo rat (*Dipodomys ingens*)

Gray wolf (*Canis lupus*)

Grizzly bear (*Ursus arctos*)

Species addressed in the Biological Opinion[a]:

Hualapai Mexican vole (*Microtus pennsylvanicus hualpaiensis*)
Jaguarundi (*Herpailurus (=Felis) yagouaroundi cacomitli*)
Jaguar (*Panthera onca*)
Key Largo cotton mouse (*Peromyscus gossypinus allapaticola*)
Key Largo woodrat (*Neotoma floridana smalli*)
Lower Keys rabbit (*Sylvilagus palustris hefneri*)
Louisiana black bear (*Ursus americanus luteolus*)
Morro Bay kangaroo rat (*Dipodomys heermanni morroensis*)
Ocelot (*Leopardus (=Felis) pardalis*)
Perdido Key beach mouse (*Peromyscus polionotus trissyllepsis*)
Point Arena mountain beaver (*Aplodontia rufa nigra*)
Salt marsh harvest mouse (*Reithrodontomys raviventris*)
San Joaquin kit fox (*Vulpes macrotis mutica*)
Silver rice rat (*Oryzomys palustris natator*)
Southeastern beach mouse (*Peromyscus polionotus niveiventris*)
Stephen’s kangaroo rat (*Dipodomys stephensi*)
Tipton kangaroo rat (*Dipodomys nitratoides nitratoides*)
Utah prairie dog (*Cynomys parvidens*)

Birds:

Atwater’s prairie chicken (*Tympanuchus cupido attwateri*)
Audubon’s crested caracara (*Polyborus plancus audubonii*)
Hawaiian coot (*Fulica americana alai*)
Hawaiian crow (*Corvus hawaiiensis*)
Hawaiian duck (*Anas wyvilliana*)
Hawaiian hawk (*Buteo solitarius*)
Mariana crow (*Corvus kubaryi*)
Mississippi sandhill crane (*Grus canadensis pulla*)
Nene [Hawaiian goose] (*Branta (=Nesochen) sandvicensis*)
Puerto Rican plain pigeon (*Columba inornata wetmorei*)
San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*)
San Clemente sage sparrow (*Amphispiza belli clementeae*)
Whooping crane (*Grus americana*)
Yellow-shouldered blackbird (*Agelaius xanthomus*)

Reptiles:

Species addressed in the Biological Opinion[a]:

- Puerto Rican boa (*Epicrates inornatus*)
- Virgin Island tree boa (*Epicrates monensis granti*)
- Eastern indigo snake (*Drymarchon corais couperi*)

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[a] scientific names are from the U.S. Fish and Wildlife Service's *Endangered and Threatened Wildlife and Plants*, 50 CFR 17.11 and 17.12, current as of December 31, 1998

USDA **United States Department of Agriculture** **Forest Service** **Rocky Mountain Region**

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File Code: 1310; 2020
Date: May 19, 2017

Wyoming County Commissioners Association
PO Box 86
Cheyenne, WY 82003

Dear Wyoming County Commissioners Association:

I wanted to personally thank you for hosting the recent tour on Thunder Basin National Grasslands. The opportunity to view the situation in person, as well as being able to engage with some of the Permittee's directly, was extremely valuable and has helped us to lay the groundwork for being able to move forward with future management on several of the issues that were identified. I also very much appreciated the participation of the permittees and the staff from the different Wyoming State Agencies. I know how valuable everyone's time is and to dedicate several days to this effort clearly demonstrates the level of concern that exists.

As we discussed, the Regional Office has worked with the Forest and District to identify both short term and long term work to be completed. The following is the current list of actions that we have identified:

Short Term Actions:

- No dusting for plague control will occur this season on federal lands within the Grassland.
- The Forest will increase acres treated this year for Prairie Dog control focusing on the boundary areas and the identified buffers around dwellings.
- The Regional Office is working with the Forest to identify maximum flexibility for options such as supplemental feeding, restoration work to aid in the recovery of impacted areas, invasive species control (cactus, etc).
- The Regional Office is looking into the appropriate use of Rozol on Forest Service lands in Thunder Basin.

Long Term Actions:

- The Regional Office is reviewing options for a potential management plan amendment regarding Black Footed Ferrets. The assessment will include the level of NEPA required, timeline, and staffing needs.

This is by no means a complete list of the work we will be carrying out, but it does reflect the majority of the areas that we discussed during the tour. Please accept my sincere appreciation for your commitment to working with us on these issues and for allowing us the opportunity to redeem our responsibility to all of you that operate on Thunder Basin and to the lands that we have been given responsibility for managing. Together I know we can get to a better place.

Sincerely,

Brian Ferebee

BRIAN FEREBEE
Regional Forester

cc: Governor Mead, Dennis Jaeger, Sandy Henning

esa ECOSPHERE

The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle

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Abstract. The Great Plains of North America evolved with significant influence from bison (*Bison bison*), but is presently dominated by cattle (*Bos taurus*). While there are a variety of opinions concerning differences between these two species, there is a lack of scientific comparisons, including those that incorporate important ecological variation. We developed a framework to study and compare the grazing behavior and effects of bison and cattle within grassland ecosystems. Environmental (e.g., resource distribution, disturbance) and animal (e.g., number, social organization) factors play a critical role in determining grazing effects and should be incorporated into discussions that compare the effects of bison and cattle. Using this framework we specifically compare the grazing behavior of both species in tallgrass prairie and discuss the implications of these differences in the context of conservation. We collared bison and cattle with global positioning systems and used resource selection functions to estimate the importance of various environmental factors on site selection. Both species preferred recently burned areas and avoided steeper slopes. Cattle selected areas that were closer to water, while bison were not limited by distance to water; cattle also preferred areas with woody vegetation, while bison avoided them. Incorporating broad scale environmental complexity allows for an effective comparison of ecological differences between bison and cattle. While there are similarities and differences in these species, a comprehensive analysis of all conditions and scenarios is not possible. It is clear, however, that the greatest differences between these species will likely be evident from broad scale studies across complex landscapes. In addition to species, conservation and land managers need to consider other environmental factors that are critical to grazing effects and overall conservation.

Key words: fire; grassland; grazing; herbivory; restoration; species comparisons; tallgrass prairie.

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INTRODUCTION

The role of herbivores in grassland ecosystems has been an important topic debated by ecologists and ecosystem managers for more than a century. The Great Plains of North America are central to this discussion as most flora and fauna evolved with significant impact from large herbivores and other disturbances (Axelrod 1985, Anderson 2006). Until their near extirpation in the late 1800s, American Bison (*Bison bison*) were keystone herbivores within the Great Plains, sharing complex landscapes with other herbivores and predators for nearly 10,000 years (Knapp et al. 1999, Anderson 2006). Since their near extinction, the vast and complex landscapes that contained the roaming herds have been replaced by fragmented agricultural lands where domestic cattle are the dominant grazers. Restoration and conservation of bison has been pursued by private citizens, conservation organizations, and government agencies with a primary goal of conserving the species and restoring critical ecosystem processes and functions.

Grazing by large herbivores can affect a system in many different ways (Milchunas et al. 1988, Augustine and McNaughton 1998, Anderson et al. 2006). The effects of grazing are often viewed in isolation of each other, removing all complexity and variation besides that of grazing. Such work has enhanced the understanding and management of grasslands. The evolutionary effects of grazing, however, are much more complex than traditional, small scale experimental designs can replicate (Levin 1992, Fuhlendorf et al. 2009). Grazing is a dynamic process that interacts with complex landscapes to form disturbance patterns that are critical to many ecosystem functions, including biodiversity (Collins et al. 1998, Tews et al. 2004). Because of this, the effects of grazing are influenced by many factors, including those associated with animals and the environment.

The species of animal alone is not the only determinant of grazing effects. Age, sex, number, and social organization of animals contribute to altering behavior and ecological influences. In addition to the structure of the grazer community, environmental factors (e.g., disturbances, climate, predation, resources) will also contribute to grazing effects. When discussing grazing or grazing behavior, a traditional reductionist approach is to focus on one factor without considering the complexity of other factors. In the Great Plains of North America, ecologists, conservation biologists, and land managers have studied and debated the effects of grazing by bison and domestic cattle (*Bos taurus*), often without including other interacting factors (Hartnett et al. 1997, Steuter and Hidinger 1999). Common managerial differences associated with bison and cattle also confound differences in effects between the two species (Towne et al. 2005). Cattle herds are often associated with ranches that are based on commodity production, where animals are commonly separated for most of the year based on sex or age (e.g., cows and calves, bulls). In the Great Plains of North America, cattle are rarely, if ever, managed as wildlife or with a conservation focus. Bison, on the other hand, may be managed as either production or conservation herds.

While similarities and differences between cattle and bison are widely discussed and debated, the peer reviewed literature comparing the two is largely inconclusive. For example, in popular press, government reports, and scientific literature, it is often stated that bison spend less time near water or riparian areas than cattle (Manning 1995, Hartnett et al. 1997, Fritz et al. 1999, Reynolds et al. 2003, National Park Service 2009). Indeed, van Vuren (1982) found a greater percentage of observations of cattle closer to water than bison. Unfortunately, it is apparent that the confounding management strategies of the two species were not taken into account, specifically with regard to stocking rate or animal density: "a herd of about 300 wild bison . . . shares its summer range with several hundred range cattle" (van Vuren 1982). With no clear definition of how many animals were present or specific management plans for each species, a reliable conclusion cannot be made. Direct comparisons of foraging ecology or behavior between bison and cattle have also been minimal. Plumb and Dodd (1993) found that in general, bison spent less time feeding with shorter grazing bouts than cattle, but had greater number of bouts per day.

We argue that recognizing ecological differences between bison and cattle would be best studied on large, complex landscapes that do not limit behavior to finer scales (Holland et al. 2004, Boyce 2006, Bowyer and Kie 2006). Incorporating landscape variability will allow for a more effective comparison of grazing behavior and effects between bison and cattle, as animals can interact with environmental factors that contribute to grazing effects. We describe the design, results, and limitations of a current study comparing bison and cattle behavior on complex landscapes that include other disturbances (e.g., fire). We then develop a conceptual model to facilitate the discussion of the conservation value of reintroducing bison within human dominated landscapes of the Great Plains.

METHODS

The Tallgrass Prairie Preserve: a model for experimental design

The Nature Conservancy Tallgrass Prairie Preserve, located in northeast Oklahoma, USA, is a 16,000 ha natural area that is managed for biodiversity and heterogeneity (Hamilton 2007). The preserve lies at the southern end of the Flint Hills of the Great Plains. Vegetation is classified as tallgrass prairie, with small patches of cross timbers forest. Dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Crosstimbers vegetation is dominated by *Quercus stellata* Wang. and *Q. marilandica* Münchh. Precipitation and various climate measurements are measured on site by an Oklahoma Mesonet station (Brock et al. 1995). Total precipitation for April through September for 2009 and 2010 (time period of study) was 64.7 and 72.5 cm, respectively. Long term mean total for April through September is 62.2 cm (14.94 standard deviation).

Within the site, there is one large bison unit (9532 ha) and seven smaller cattle units (430–980 ha) (Fig. 1). Only perimeter fences are present and animals are free to roam within their respective units. There is minimal handling of both bison and cattle with no supplemental feeding. Bison are maintained in their respective unit all year; herd size is approximately 2,300 animals. Sex ratio of the bison herd is approximately seven females per male; ages of females range from 0–10 years, while males are 0–6 years. Cattle units are stocked with stocker steers approximately one year old (mixed European breeds); cattle are only present April through September. Cattle herds vary with each unit, ranging from 169 to 463 animals. Bison and cattle units are stocked with similar moderate stocking rates (bison: 2.1 AUM/ha; cattle: 2.4 AUM/ha). The entire preserve is managed extensively with fire and in such way that fire and grazing are allowed to interact (Hamilton 2007, Fuhlendorf et al. 2009). Bison and cattle units are shifting mosaics with fire occurring in discrete portions of the landscape (Fig. 1). Fire-grazing interactions become present as animals select between recently burned areas and those with greater time since fire (Archibald et al. 2005, Fuhlendorf et al. 2009).

To specifically examine herbivore site selection, we deployed global positioning system (GPS) collars on seven female bison (four to six years in age) from November 2008 through November 2010 and seven cattle (steers, one year in age; one per unit) from April through September of 2009 and 2010. For bison, GPS batteries were replaced and new animals chosen in November 2009; for cattle, new animals were chosen and new batteries used in April 2010. We recorded location information of animals at two different frequencies, alternately weekly from 12 minutes to one hour. Schedule of GPS fixes was equal for bison and cattle. We imported all GPS location data into a spatially enabled database (PostgreSQL/PostGIS) and reduced bison data to match that of cattle (April–September). We mapped treatment unit perimeters, fire histories, and water sources (ponds and streams) with handheld GPS units, aerial photographs, and United States Geological Survey 7.5 minute topographic maps. Slope and aspect were calculated from digital elevation models for the area (United States Geological Survey; 10 m resolution). We transformed aspect data by simple trigonometric functions; two variables were created, northing = cosine(aspect) and easting = sin(aspect). Herbaceous and woody vegetation was determined for the site using a GeoEye-1 satellite image acquired September 20, 2009.

We compared similarity of units by randomly placing 1,000 sampling points within each unit. At each sampling point, distance to water, distance to patch edge, distance to woody vegetation, slope, northing, and easting were calculated. Measured characteristics among animal units were compared individually using analysis of variance and did not differ between units ($P > 0.05$). We used Ivlev electivity indices (Ivlev 1961, Jacobs 1974) to evaluate the use of riparian areas by bison and cattle. Riparian areas were defined by putting a 20 and 40 m buffer around all mapped water sources. We calculated electivity indices using the formula $E_i = (r_i - p_i)/(r_i + p_i)$ where r_i is the fraction of GPS locations recorded in a riparian area by animal i and p_i is the fraction of area enclosed by the sum of buffers available to animal i. A value of +1 indicates complete preference to riparian areas, while a value of −1 indicates complete avoidance. Indices were calculated for each collared bison

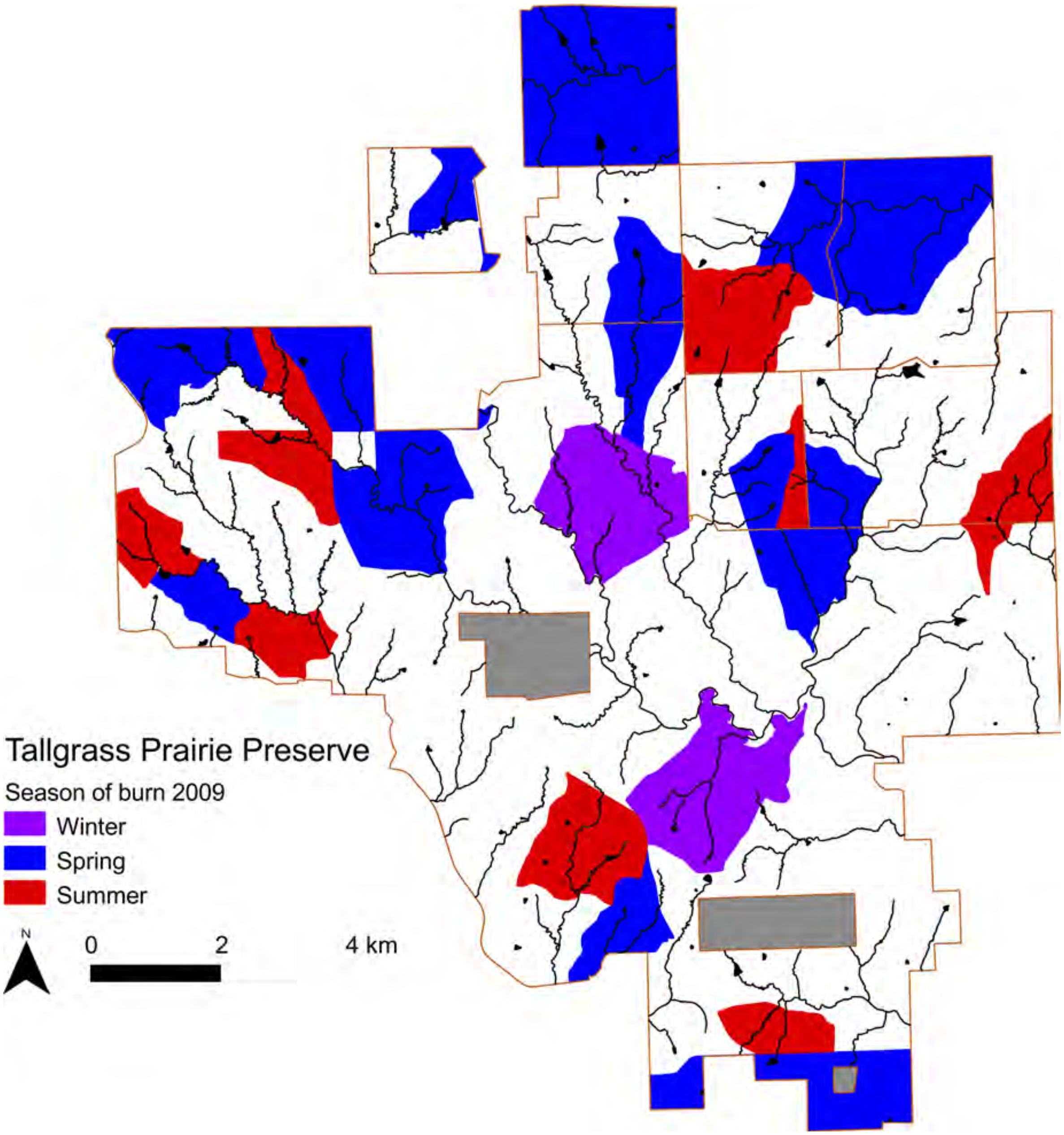

Fig. 1. Map of prescribed fire and water distribution within bison and cattle units at The Nature Conservancy Tallgrass Prairie Preserve, OK, USA, September 2009. Solid orange lines represent perimeter fences and delineate units. Black interior lines and areas represent water sources. Gray areas inside bison unit represent inholdings which bison cannot access. The large southern unit is 9532 ha in size and contains bison year round. The northern units are 430–980 ha in size and contains mixed European breeds of cattle April-September. Differing colors represent season of burn for 2009 and illustrate the patchiness of fire. Patches from previous years are not shown, but vary from one to five years since fire. Grazing animals have free access to all burns within their respective units (no internal fences present).

and cattle individual, separating water sources into ponds, streams, and pond/stream combination. Indices between bison and cattle were compared for each size riparian area (i.e., 20 and 40 m) using a *t*-test. We also used Ivlev electivity indices to compare bison and cattle preferences for recently burned areas (six months or less since fire). We calculated indices for each collared animal based upon recently burned area available; we compared indices using a *t*-test.

To examine the influence of environmental factors on the grazing behavior of bison and cattle, we estimated resource selection functions using mixed-effect logistic regression models (used/available design; Boyce et al. 2002, Manly et al. 2002). To depict available habitat, we created five random locations for each observed location. We calculated the amount of time since fire, distance to water, distance to fire patch edge, slope, northing, and easting for all locations. We also classified each location as herbaceous or woody vegetation. To determine if the presence of woody vegetation is confounded with water sources (i.e., the presence of woody vegetation is primarily near water sources), we quantified the distribution of woody vegetation around water sources. The percentage of woody vegetation within 20 and 40 m of water sources across the site was 3% and 7%, respectively. Furthermore, we examined variables for collinearity and found none ($r^2 < 0.27$ for all variable combinations), indicating that variables are not confounding with one another (i.e., woody vegetation is not limited near water sources). To account for variation among individual animals within resource selection functions, individuals were included as a random intercept within logistic regressions. To account for fire availability among units and potential response variation to fire, time since fire and its interaction with other variables (e.g., time since fire × distance to water; see below) were included as random slopes within logistic regressions (Gillies et al. 2006).

We created models using various combinations of environmental factors; as the influence of time since fire is likely to be highly influential (Vinton et al. 1993, Fuhlendorf and Engle 2004, Archibald et al. 2005), we included interaction terms for this variable with all others individually (i.e., time since fire × distance to water, time since fire × slope, etc.). In all models with interaction terms, main effects of both variables were included. To allow for comparison of environmental factors and to more easily interpret interaction terms, we standardized variables by subtracting the mean and dividing by the standard deviation (Gelman and Hill 2007). We compared and ranked models using Akaike information criterion (AIC; Burnham and Anderson 2002). We used bootstrapping procedures to further estimate the precision of resource selection coefficients of the top ranked model. We calculated 95% confidence intervals of coefficients after 1,000 iterations of randomly sampled datasets. To further examine variation among individual animal behavior, we calculated resource selection functions for each animal per year (28 animals total) using top ranked models. We performed all analyses in R (R Development Core Team 2009) with additional use of the *lme4* (Bates and Maechler 2010), *doMPI* (Weston 2009), *foreach* (Revolution Computing 2009) and *Rmpi* (Yu 2010) packages.

RESULTS

Of bison locations, 9 and 15% fell within riparian areas of size 20 and 40 m, respectively (ponds and streams combined). Of cattle locations, 13 and 20% fell within riparian areas of size 20 and 40 m, respectively. Mean Ivlev electivity indices of riparian areas varied significantly between bison and cattle with all water sources and riparian area sizes ($P < 0.01$; Fig. 2). Cattle had a greater preference for ponds (Fig. 2A), while bison avoided streams (Fig. 2B). When ponds and streams were combined, bison had a small avoidance of water, while cattle had a greater preference for it (Fig. 2C). These data show the difference between bison and cattle in their use of water and riparian areas, in similar fire-managed landscapes with abundant water.

Bison and cattle strongly preferred recently burned patches (Table 1). Mean percentages of GPS locations in areas with six months or less since fire did not vary between bison and cattle ($P = 0.11$) With bison, 68% of locations were found in recently burned areas (less than six months), while cattle were 58%. The amount of area burned within six months was approximately 25% of the landscape in both bison and cattle units. Bison and cattle were nearly three times likely to be in a burned area than by random

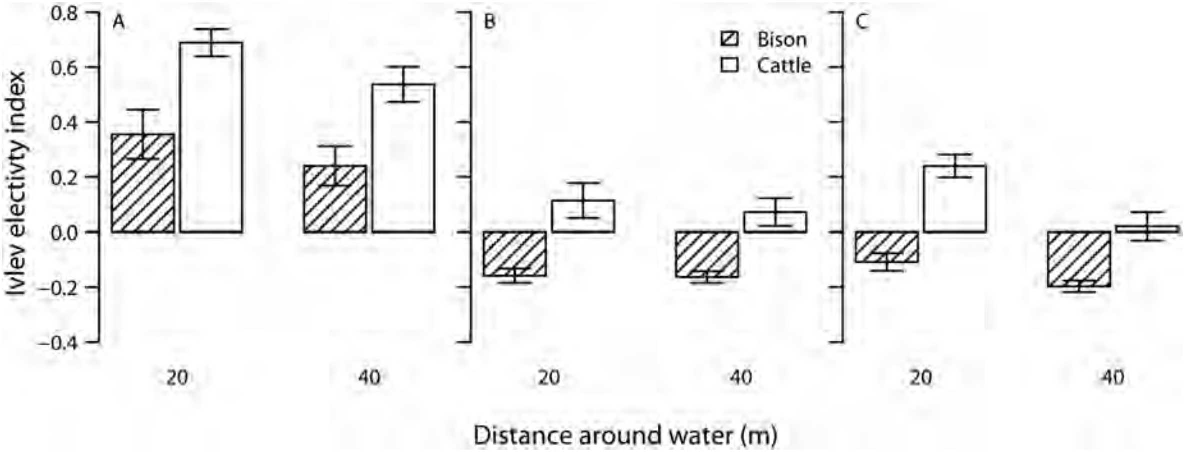

Fig. 2. Ivlev electivity indices for riparian areas, separated by bison and cattle at the Tallgrass Prairie Preserve, OK, USA. Bars are means (n = 14; animals), error bars are one standard deviation. Potential values range from −1 (complete avoidance) to +1 (complete preference). Distance around water indicates the size of buffer placed around water sources. A) Ivlev electivity indices for ponds only, separated by bison and cattle. Cattle preferred riparian pond areas more than bison. B) Ivlev electivity indices for streams only, separated by bison and cattle. Cattle preferred riparian stream areas more than bison; bison demonstrated a small avoidance to riparian stream areas. C) Ivlev electivity indices for ponds and streams combined, separated by bison and cattle. Cattle preferred all riparian areas more than bison; bison demonstrated a small avoidance to all riparian areas. Mean electivity indices of riparian areas varied significantly between bison and cattle for all water sources and buffer sizes ($P <$ 0.01).

Table 1. Percentage of individual bison and cattle locations and annual means and confidence intervals (95%; bottom row) in recently burned areas (six months or less) at the Tallgrass Prairie Preserve, OK, USA, April through September 2009 and 2010.

Bison 2009	Bison 2010	Cattle 2009	Cattle 2010
68.3	64.1	78.6	42.4
71.5	59.1	55.7	88.7
69.1	66.9	77.5	100.0†
68.8	67.8	60.8	73.2
75.3	69.0	25.0	55.0
66.2	65.2	100.0†	37.4
75.1	75.1	67.6	40.6
70.6 (2.6)	66.7 (3.6)	60.9 (15.8)	56.2 (16.5)

†Due to fire patch design; not included in mean or confidence interval calculation.

chance alone. Mean Ivlev electivity indices of recently burned areas were 0.57 (0.01) and 0.43 (0.15) for bison and cattle, respectively (standard deviations in parentheses); indices did not differ between species ($P = 0.12$).

Estimation of resource selection functions permitted a detailed examination of environmental factors that influence selection behavior. Of models examined, the combination of interaction terms of time since fire with all variables (less northing and easting) appeared to have the best fit for both bison and cattle (Table 2). Resource selection functions for bison revealed that time since fire had the strongest influence in determining site selection. Furthermore, bison tended to avoid steeper slopes and wooded areas. Distance to water did not influence selection (Table 3). Interactions of time since fire with other environmental factors indicates the connectedness of fire with grazing behavior. The influence of time since fire increased as slope and distance to patch edge increased; conversely, the influence

Table 2. The difference in Akaike information criterion (ΔAIC) and the number of parameters (K) for varying models of resource selection for bison and cattle at the Tallgrass Prairie Preserve, OK, USA; model parameters include distance to water (*water*; m), distance to patch edge (*edge*; m), slope (*slope*; degrees), northing (*north*; degrees), easting (*east*; degrees), wooded area (*wood*), and time since fire (*tsf*; days).

Model	K	ΔAIC
Bison		
tsf × *water* + *tsf* × *slope* + *tsf* × *edge* + *tsf* × *wood* + *tsf* × *north* + *tsf* × *east*	15	1.8
tsf × *water* + *tsf* × *slope* + *tsf* × *edge* + *tsf* × *wood* + *north* + *east*	13	0.00
tsf × *water* + *tsf* × *slope* + *tsf* × *edge* + *tsf* × *wood*	10	2.7
tsf × *water* + *tsf* × *slope* + *tsf* × *edge* + *wood*	11	3.8
tsf × *water* + *tsf* × *slope* + *edge* + *tsf* × *wood*	10	4006.4
tsf × *water* + *slope* + *tsf* × *edge* + *tsf* × *wood*	10	882.4
water + *tsf* × *slope* + *tsf* × *edge* + *tsf* × *wood*	10	505.7
tsf + *water* + *slope* + *edge* + *wood*	7	6328.7
Cattle		
tsf × *water* + *tsf* × *slope* + *tsf* × *edge* + *tsf* × *wood* + *tsf* × *north* + *tsf* × *east*	15	3.26
tsf × *water* + *tsf* × *slope* + *tsf* × *edge* + *tsf* × *wood* + *north* + *east*	13	0.00
tsf × *water* + *tsf* × *slope* + *tsf* × *edge* + *tsf* × *wood*	10	2.71
tsf × *water* + *tsf* × *slope* + *tsf* × *edge* + *wood*	11	15.89
tsf × *water* + *tsf* × *slope* + *edge* + *tsf* × *wood*	10	126.34
tsf × *water* + *slope* + *tsf* × *edge* + *tsf* × *wood*	10	42.78
water + *tsf* × *slope* + *tsf* × *edge* + *tsf* × *wood*	10	329.18
tsf + *water* + *slope* + *edge* + *wood*	7	451.37

Notes: We included main effects in all models with interaction terms. Interaction terms represented with ×.

Table 3. Estimated resource selection function coefficients of the top ranked model for bison and cattle at the Tallgrass Prairie Preserve, OK, USA; model parameters include distance to water (water; m), distance to patch edge (edge; m), slope (slope; degrees), northing (north; degrees), easting (east; degrees), wooded area (wood), and time since fire (tsf; days).

Parameter	Estimate†	SE	Z value	*P*	CI‡
Bison					
intercept	−1.8460	0.120	−15.34	<0.01	(−1.8513, −1.8384)
time since fire	−1.5521	0.353	−4.40	<0.01	(−1.5538, −1.5509)
distance to water	0.0324	0.007	4.51	<0.01	(0.0316, 0.0328)
slope	−0.5785	0.011	−49.59	<0.01	(−0.5793, −0.5778)
distance to patch edge	−0.3351	0.009	−35.87	<0.01	(−0.3360, −0.3344)
woody vegetation	−1.9116	0.077	−24.53	<0.01	(−1.9164, −1.9092)
northing	−0.0117	0.005	−2.33	0.02	(−0.0120, −0.0115)
easting	0.0246	0.005	4.87	<0.01	(0.0242, 0.0251)
time since fire × distance to water	0.1548	0.007	19.48	<0.01	(0.1543, 0.1550)
time since fire × slope	−0.3814	0.013	−28.23	<0.01	(−0.3818, −0.3809)
time since fire × distance to patch edge	−0.5412	0.011	−48.86	<0.01	(−0.5420, −0.5408)
time since fire × woody vegetation	0.0509	0.041	1.24	0.21	(0.0478, 0.0549)
Cattle					
intercept	−0.8892	0.644	−1.38	0.16	(−0.8963, −0.8824)
time since fire	−1.2611	0.313	−4.03	<0.01	(−1.2621, −1.2602)
distance to water	−0.0768	0.006	−11.11	<0.01	(−0.0785, −0.0755)
slope	−0.1696	0.007	−21.50	<0.01	(−0.1699, −0.1691)
distance to patch edge	−0.5019	0.011	−42.44	<0.01	(−0.5025, −0.5015)
woody vegetation	1.4398	0.053	27.16	<0.01	(1.4390, 1.4404)
northing	−0.0044	0.005	−0.84	0.40	(−0.0048, −0.0040)
easting	−0.0109	0.005	−2.08	0.03	(−0.0112, −0.0107)
time since fire × distance to water	−0.0514	0.059	−2.08	0.03	(−0.0520, −0.0511)
time since fire × slope	0.0199	0.049	0.40	0.68	(−0.0210, −0.0190)
time since fire × distance to patch edge	−0.2667	0.219	1.22	0.22	(−0.2692, −0.2648)
time since fire × woody vegetation	0.4213	0.382	1.10	0.27	(0.4201, 0.4219)

†Standardized variables are shown for coefficient comparison and interaction term interpretation.
‡Confidence interval (95%) calculated from bootstrapping procedures (1,000 iterations).

of time since fire decreased as woody vegetation and distance to water increased. This decrease is minimal due to the initial strong influence of fire. The probability of selection for bison, based upon time since fire, distance to water, and the interaction of those two factors, is displayed in Fig. 3. In recently burned areas, bison avoid water slightly; in areas with greater time since fire, bison are not influenced by water.

Similar to bison, cattle also selected recently burned areas and avoided steeper slopes. Unlike bison, however, the most influential environmental factor was the preference of woody vegetation. Moreover, cattle appeared to minimize distance to water, opposite that of bison (Table 3). Interactions of time since fire with other variables further shows the importance of fire to understanding grazing within these ecosystems. As distance to water and patch edge increase, so does the influence of time since fire; the presence of woody vegetation, however, decreases the influence of time since fire. The probability of selection for cattle, based upon time since fire, distance to water, and the interaction of the two, is displayed in Fig. 4. Cattle minimize their distance to water in both recently burned areas and areas with greater time since fire.

Resource selection functions for individual animals revealed variation in site selection (Table 4). Though individual animals generally followed trends indicated by the population model, cattle tended to be more variable in their response to environmental factors. Individual bison and cattle still strongly preferred recently burned areas (minimizing the amount of time since fire), but the response of cattle varied considerably among individuals. All individual cattle minimized their distance to water, while only three bison did so. Other factors, including interactions with time since fire, varied among animals. Because different animals were chosen each year, we cannot separate the variation among animals and the variation between years.

Discussion

The design of this study more effectively permits comparisons between bison and cattle, both in examining grazing behavior differences between the species (results presented here) and their ecological effects (e.g., plant response, water quality, etc.; data not collected). Our design incorporates more of the variability found in complex landscapes than previous studies, allowing animals to interact and respond to variation and complexity across the landscape. Bison and cattle had similarities in some aspects of their behavior. Both species had a strong preference for recently burned areas, similar to separate studies of the individual species (Coppedge et al. 1998, Fuhlendorf and Engle 2004). Along with similarities we also identified two key differences. Cattle preferred areas with woody vegetation, while bison avoided them. This likely plays a critical role in thermal regulation, with woody canopy cover providing shade from solar radiation. Detailed mapping of the thermal environment is required to determine the influence of heat on the grazing behavior of bison and cattle. Additionally, because location information obtained by the GPS does not differentiate between grazing or resting, it is unclear if the preference for woody vegetation is a result of grazing or resting behavior. It does show, however, behavioral preferences and differences that are likely to influence both selection and grazing decisions, especially when studying behavior at broad spatial scales.

Selection for sites closer to water was also greater in cattle than bison; bison appeared to maximize their distance to water while cattle minimized it. These differences occurred in a well watered landscape and may be even more important in lands with greater distance between water sources. Though water included ponds and streams, ephemeral water sources were not included due to difficulty in measuring them at this spatial scale. Differences in use of ephemeral water between bison and cattle may explain measured differences. Additionally, both bison and cattle distribution and behavior may be influenced by precipitation patterns (Lott 2002, McAllister et al. 2006). At broader scales such as the Tallgrass Prairie Preserve, variability in spatial precipitation patterns may exist (Augustine 2010). Though not quantified, spatial variability in precipitation would likely influence animal distribution indirectly through vegetation responses and ephemeral water sources.

Although we did not collect data on ecological implications of grazing, it is likely that distribution differences between bison and cattle would

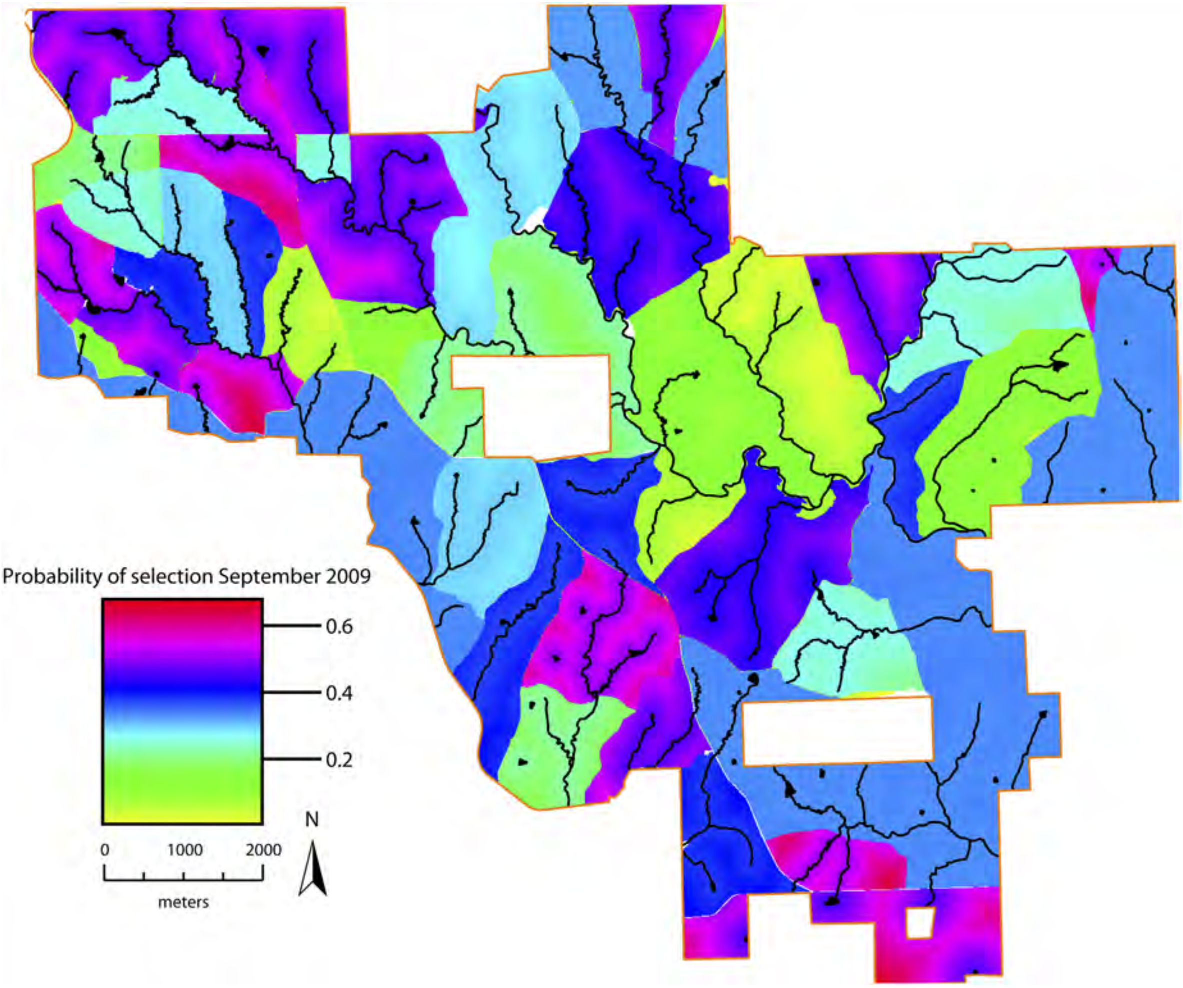

Fig. 3. Probability of selection for bison at the Tallgrass Prairie Preserve, OK, USA September 2009. Probabilities presented as a function of time since fire, distance to water, and their interaction. Black interior lines and areas represent water sources. Solid orange lines represent perimeter fences. Refer to Fig. 1 for recently burned areas. Bison prefer recently burned areas and do not minimize their distance to water. Due to the preference of recently burned areas, probabilities will change as fire is applied and moved around the landscape.

result in contrasting effects. The preference or focusing of grazing in a particular area (large or small) will influence vegetation community and characteristics. The continued attraction of both bison and cattle to recently burned areas alters vegetation structure which affects biodiversity (Fuhlendorf et al. 2006), fire behavior (Leonard et al. 2010), invasive species populations (Cummings et al. 2007), invertebrate populations and communities (Engle et al. 2008), and nutrient cycling and distribution (Anderson et al. 2006). The preference of riparian and woody vegetation areas by cattle will also likely result in vegetation and system changes. Reduced herbaceous cover, biomass, and productivity generally result from cattle grazing within riparian areas (Kauffman et al. 1983, Clary 1995, Belsky et al. 1999). Preference for water sources may also affect stream bank morphology, hydrology, and water quality (Kauffman and Krueger 1984, Trimble and Mendel 1995, Belsky and Blumenthal 1997). Concentration of livestock around ponds and streams may also likely increase nutrient concentrations (Schepers and Francis 1982, Belsky et al. 1999). We note, however, that direct comparisons of bison and cattle grazing effects on riparian

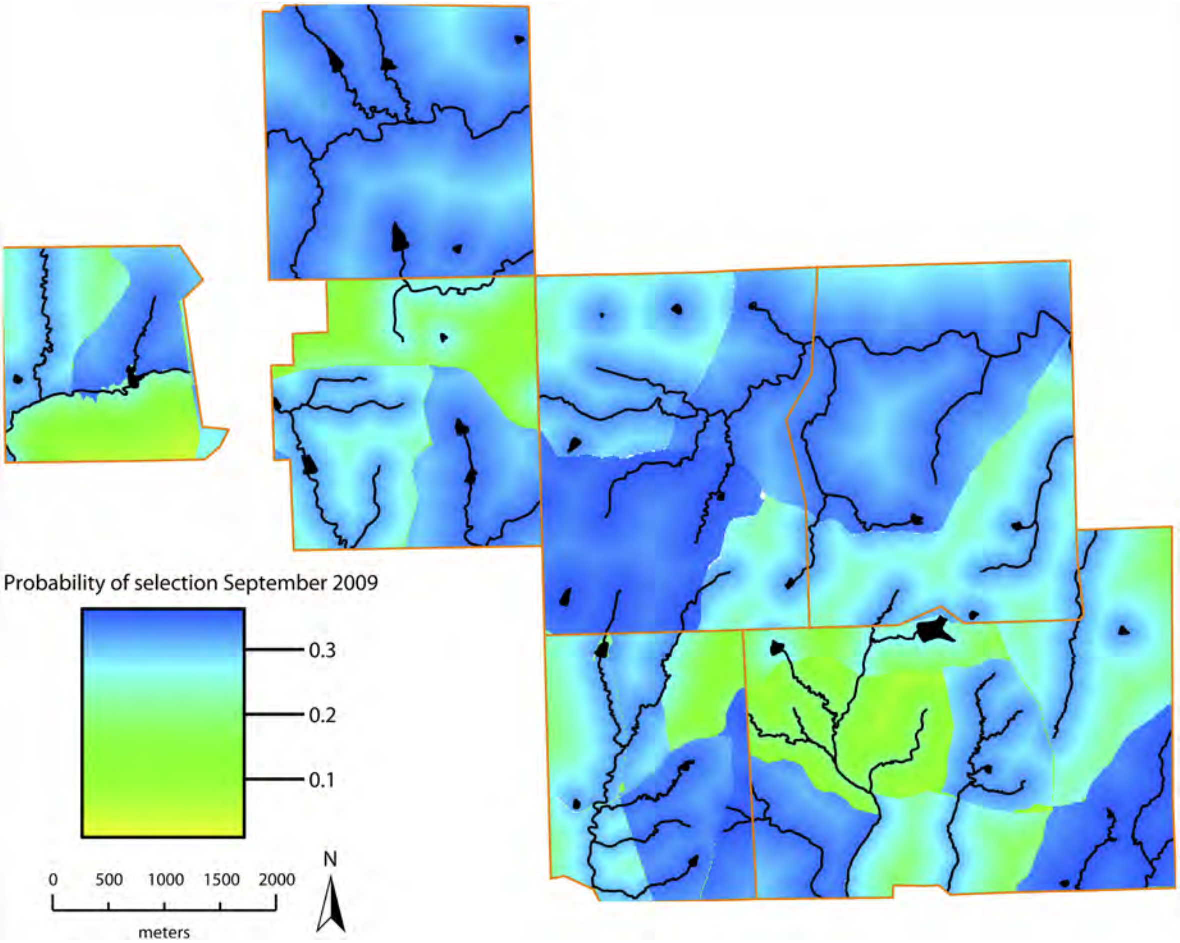

Fig. 4. Probability of selection for cattle at the Tallgrass Prairie Preserve, OK, USA September 2009. Probabilities presented as a function of time since fire, distance to water, and their interaction. Black interior lines and areas represent water sources. Solid orange lines represent perimeter fences. Refer to Fig. 1 for recently burned areas. Cattle prefer recently burned areas and minimize their distance to water. Due to the preference of recently burned areas, probabilities will change as fire is applied and moved around the landscape.

processes are largely lacking.

It is difficult to account for the many factors that may create differences or similarities between bison and cattle, and like all studies of processes on complex landscapes, this study is not without limitations. Though stocking rates were similar between bison and cattle units, cattle were only present during the growing season (April–September), while bison remained throughout the year. Differences in the social and temporal organizations of cattle and bison herds may also confound differences. The bison herd was a mixture of males and females of various ages grazing together, while cattle herds were yearling stocker steers. A yearlong, cow-calf cattle operation would permit even better comparisons between the two species, particularly with regard to ecological effects. Though treatment units were large and incorporated landscape complexity, they were not of equal size. We could expect that animal behavior would be sensitive to and vary with available area. Smaller units would limit animal movement and behavior, restricting selection and interaction with other environmental factors. Available area would be important particularly regarding cattle preference for water, as smaller units would constrain animals closer to water. While cattle

Table 4. Estimated resource selection function coefficients† of the top ranked model for individual bison and cattle at the Tallgrass Prairie Preserve, OK, USA each year of study (2009 and 2010); model parameters include distance to water (water; m), distance to patch edge (edge; m), slope (slope; degrees), northing (north; degrees), easting (east; degrees), wooded area (woody), and time since fire (tsf; days).

Year	tsf	water	slope	edge	woody	north	east	tsf × wtr	tsf × slp	tsf × edge	tsf × wdy
Bison											
2009	−1.69	−0.01	−0.72	−0.55	−2.44	0.01	0.06	0.12	−0.48	−0.78	−1.85
2009	−1.29	0.20	−0.48	−0.12	−2.45	0.00	0.03	0.31	−0.22	−0.34	−1.64
2009	−1.74	0.19	−0.61	−0.50	−1.22	0.01	−0.01	−0.05	−0.35	−0.78	−0.47
2009	−1.16	0.00	−0.63	−0.43	−1.55	−0.03	0.06	0.15	−0.58	−0.59	−0.93
2009	−1.91	0.23	−0.45	−0.40	−2.45	−0.03	0.02	0.30	−0.31	−0.64	−2.38
2009	−1.35	−0.02	−0.62	−0.14	−2.59	−0.02	0.02	0.11	−0.37	−0.39	−2.23
2009	−1.57	0.10	−0.56	−0.36	−1.46	−0.03	0.00	0.00	−0.37	−0.43	−1.19
2010	−1.38	0.13	−0.51	−0.07	−1.38	0.03	0.00	0.20	−0.08	−0.26	0.30
2010	−1.16	0.13	−0.49	−0.14	−1.35	0.00	−0.03	0.10	−0.16	−0.22	0.27
2010	−1.37	0.06	−0.54	−0.25	−0.82	0.01	0.01	0.14	−0.17	−0.37	0.40
2010	−1.52	0.11	−0.51	−0.06	−0.71	0.01	−0.02	0.19	−0.16	−0.20	0.32
2010	−1.46	0.06	−0.57	−0.14	−0.40	0.04	−0.02	0.07	−0.07	−0.38	1.16
2010	−1.38	0.00	−0.79	−0.13	−1.59	0.02	0.00	−0.02	−0.30	−0.33	−0.11
2010	−1.79	−0.15	−0.43	−0.17	−1.21	−0.02	0.03	−0.08	−0.08	−0.32	0.11
Variation‡	0.23	0.10	0.10	0.17	0.70	0.02	0.03	0.12	0.16	0.19	1.12
Cattle											
2009	−1.70	−0.05	−0.46	−0.81	−1.66	0.04	−0.01	−0.19	−0.32	−1.20	−1.68
2009	−1.44	−0.33	−0.11	−0.87	2.74	−0.06	−0.02	0.26	0.05	−1.78	−0.23
2009	−1.16	−0.30	−0.02	−0.28	2.37	0.00	−0.01	−0.19	0.18	−0.94	0.18
2009	−0.37	−0.03	−0.15	−0.69	1.61	−0.01	0.01	−0.23	0.00	0.53	−0.47
2009	−0.36	−0.11	−0.25	−0.18	1.42	0.02	0.01	−0.09	−0.12	0.08	0.10
2009	−0.79	−0.22	−0.28	−0.12	1.24	0.00	0.00	−0.25	−0.08	0.03	0.40
2009	−3.35	−0.62	−0.15	−0.61	1.49	0.00	−0.04	−0.95	−0.04	−0.97	0.43
2010	−0.37	−0.09	−0.27	−0.07	1.60	0.01	0.00	−0.81	−0.01	0.00	0.04
2010	−2.72	−0.45	−0.42	−0.82	3.66	0.04	−0.02	−0.55	−0.47	−0.99	1.44
2010	−1.24	−0.38	−0.12	−0.37	1.86	0.05	−0.04	−0.56	0.14	−0.41	−0.72
2010	−1.59	−0.17	−0.02	−0.43	1.24	0.00	0.01	−0.39	−0.10	−0.38	−0.41
2010	−0.48	−0.29	−0.24	−0.32	2.79	−0.05	0.04	−0.44	−0.33	0.18	−0.50
2010	−2.09	−0.21	0.04	−1.18	1.31	−0.03	−0.01	−0.79	−0.03	−0.55	0.44
2010	−1.16	−0.13	−0.40	−0.41	0.82	0.00	−0.01	−0.21	−0.42	−0.39	−0.24
Variation‡	0.91	0.17	0.16	0.33	1.22	0.03	0.02	0.33	0.2	0.63	0.71

†Standardized variables are shown for coefficient comparison and interaction term interpretation.
‡Variation measured by calculating the standard deviation of coefficients within species.

units within the Tallgrass Prairie Preserve are smaller than the bison unit, they are larger than the majority of land holdings within the Great Plains; size likely did not limit the distance to water. This study also compared bison to European cattle breeds that are typical for livestock production objectives on tallgrass prairies. Other breeds of cattle are likely to respond differently (Rook et al. 2004, VanWagoner et al. 2006). Brahman or Texas longhorn breeds, for example, are likely to be adapted to more arid environments where water is limiting and may behave more similarly to bison.

In the Great Plains of North America, bison are reintroduced for primarily two objectives: species conservation and restoration of ecosystem processes. Reintroduction to conservation areas, development of private herds, and recent efforts in identifying pure herds to conserve genetics have been successful in restoring wild bison populations to many areas. Conservation of this species is a unique success story that deserves acknowledgement. Bison are also reintroduced to restore keystone effects (Knapp et al. 1999). Conservation groups as well as government agencies reintroduce bison to both small prairie remnants and large landscapes to restore historical disturbance patterns. In most cases, this is done without considering the many other factors that influence grazing behavior or effects. While the first objective for reintroduction can be accomplished by building up bison herds throughout the Great Plains, the second objective is not possible without the consideration or reintroduction of other environmental or animal factors. For example, we show that both of these herbivores have a strong preference for recently burned areas. This may suggest that the reintro-

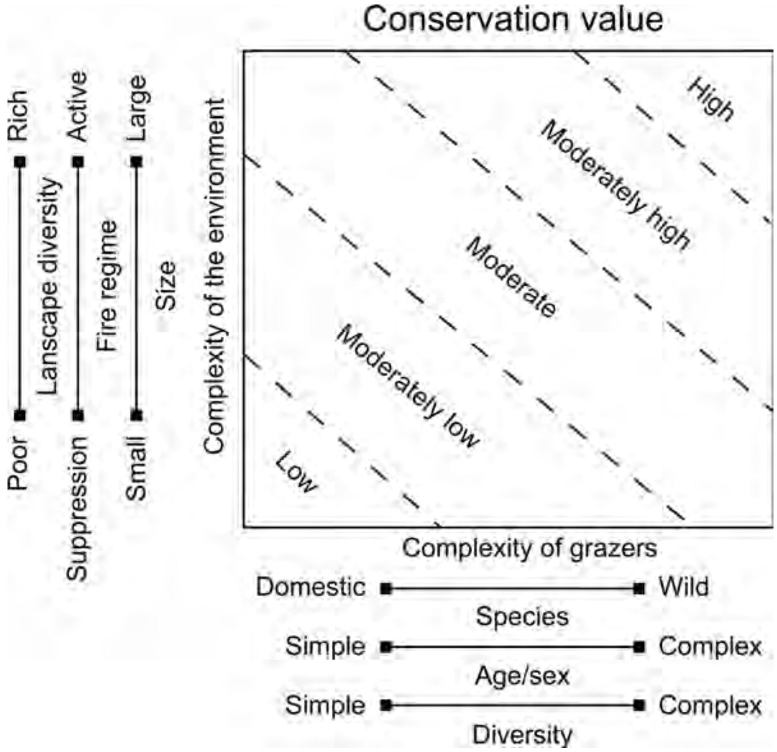

Fig. 5. Conceptual model to evaluate conservation value with respect to animal and environmental factors. Conservation value is defined as the contribution to regional conservation efforts, which includes the promotion of native plants, animals, and ecosystem processes. Species of animal alone does not automatically increase the value in regard to conservation; other factors play an important role in overall conservation value.

duction of bison, or the evaluation of differences between these species, may be largely irrelevant unless fire and other complexities are incorporated (Fuhlendorf et al. 2009). It is likely true that other factors, such as predators, would also greatly alter animal behavior and grazing effects (Ripple and Beschta 2003).

Conservation efforts regarding bison reintroduction should be evaluated to not only see if specific objectives are met, but how efforts contribute to overall conservation. We developed a conceptual model to evaluate the conservation value of different options regarding bison reintroduction (Fig. 5). We define conservation value as the contribution to regional conservation efforts, including promotion of native plants, animals, and ecosystem processes. The model is based on two primary factors that influence grazing behavior and effects, primarily complexity of grazers and the environment. Complexity of grazers refers to factors such as species, diversity, and social organization that contribute to the overall conservation value. Although this study examined only differences between two species, increasing species diversity with multiple species will add additional complexity to the system and alter the effects of grazing (du Toit and Cumming 1999, Hooper et al. 2005, Burns et al. 2009). Other native species in North American grasslands, such as prairie dogs (*Cynomys* spp.) are also important components of the system; as an example, incorporating prairie dogs will increase conservation value (Coppock et al. 1983).

The social organization of ungulates, particularly age and sex ratios, also contribute to ecosystem functioning, complexity, and conservation (Sheldon and West 2004, Gordon et al. 2004, Milner et al. 2007). Variation in animal factors will also contribute to interactions with the environment. For example, the body size of animals (also related to age and sex) influences preferences for burned areas, playing an important role in spatiotemporal heterogeneity (Wilsey 1996, Sensenig et al. 2010). Simple social organization, such as the yearling stocker steers within cattle units of this study, limit variability and decrease conservation value. With particular regard to livestock production, complexity of grazers may be improved by increasing individual variation or combing differing breeds or species (VanWagoner et al. 2006, Searle et al. 2010). Historically, bison were a keystone species, but their impacts were dependent upon how they interacted with the environment, disturbances, and other herbivores. Increasing the complexity of grazers (more species diversity, more wild herbivores, etc.) increases the conservation value, but this value is also dependent upon environmental factors. The simple replacement of domestic cattle with bison may contribute to bison conservation, but may have minimal impact on the broader conservation value of ecosystems. In an extreme example, replacing cattle with bison in a small, intensively managed, and simplified livestock production operation (e.g., a feedlot or small pasture) has little conservation value. Restoring other important processes such as fire, predation, etc. are just as important as the large herbivore upon the landscape (Ripple and Beschta 2003, Fuhlendorf et al. 2009).

Conservation value is also dependent upon the environmental complexity of the area. The majority of these factors are independent of the species of herbivore. In mesic grasslands of the Great Plains (tallgrass and mixed grass prairies), fire-grazing interactions have been shown to be a dominant driver of animal distribution and integral ecosystem process (Fuhlendorf and Engle 2004, Vermeire et al. 2004, Anderson et al. 2006). Similar to the example given above, the simple replacement of cattle with bison without a restoration of fire regimes will not result in disturbance patterns that are critical for conservation and biodiversity. In our study, time since fire was a primary driver in bison and cattle grazing behavior. The suppression of fire or the simplification of fire-grazing interactions within fire prone systems will limit conservation value, regardless of the herbivore species. Environmental factors that are critical to grazing effects and other ecosystem processes need to be accounted for in study designs that evaluate the role of grazing in conservation efforts. In North American grasslands, key environmental factors include fire regimes (Wright and Bailey 1982, Knapp et al. 1998, Brockway et al. 2002), landscape complexity and size (Herkert 1994, With et al. 2008), water distribution (Bailey et al. 1996, Augustine 2010), and woody vegetation (Archer et al. 1995, Briggs et al. 2002). These do not only influence grazing and the resulting effects, but play a broader role in ecosystem functioning. On lands with minimal environmental complexity, any differences between bison and cattle will likely contribute little to conservation value.

Grasslands are endangered worldwide (Hoekstra et al. 2005). While propositions to restore or conserve grasslands regularly focus on native herbivores (e.g., Sanderson et al. 2008), it is often overlooked that the majority of grasslands are privately owned and used for domestic livestock production (particularly true in the Great Plains of North America; Samson and Knopf 1994). Low and high conservation values can be achieved with bison or cattle. Though bison are the iconic symbol of the Great Plains of North America, and it is critical that we conserve the species, there are not enough data to confidently state that landscapes with bison are inherently better than landscapes with cattle for overall conservation or biodiversity. Both species can be mismanaged and cause degradation of habitat as well as ecological processes. Using domestic cattle to achieve some conservation objectives may be more practical or relevant, as cattle currently make up the vast majority of herbivores in many grasslands. Conservation value of productions cattle herds can be improved by increasing the size and complexity of landscape available. Allowing cattle to move at broader spatial scales and to interact with biotic and abiotic factors, may increase conservation value substantially, perhaps more so than replacing cattle with bison at finer scales. Popular management strategies that constrain animal movement and behavior (through use of fencing and rotation) may prevent many important interactions between the animal and environment, potentially reducing conservation value. As more studies effectively and appropriately compare grazing behavior and effects at broad and fine spatial scales, additional reliable conclusions will be made that may change conservation efforts or directions.

We argue that for future studies and comparisons between bison and cattle (as well as other species) it is critical that we limit our extrapolation with discussions of the abiotic and biotic environment in which these studies occur. Though it is unlikely that we will be able to conduct studies that encompass all possibilities in environmental and herbivore complexity, we must begin to contextualize our discussions and limit our inferences. From a conservation perspective it is important to understand the ecological effects of cattle grazing for livestock production, and explore approaches to alter these patterns to more effectively achieve conservation objectives. It is not productive to look for differences or similarities between bison and cattle to justify certain management objectives or agenda. In the face of the vast variability and complexity in which these species are nested within, generalizations are limited and over inferences likely.

Conservation of bison is important as an iconic species and a keystone herbivore (Knapp et al. 1999). From a broad context, however, conservation efforts need to recognize that cattle will continue to be a dominant feature on the Great Plains and grasslands worldwide, and that some conservation objectives may be met using cattle. It is critical to understand grazing behavior and ecological effects of both species in simple and complex landscapes relevant to conservation. There is an important place for species comparisons, but this is just one aspect of grassland conservation and may not be the most important for future conservation of biodiversity.

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LITERATURE CITED

Anderson, R. C. 2006. Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. Journal of the Torrey Botanical Society 133:626–647.

Anderson, R. H., S. D. Fuhlendorf, and D. M. Engle. 2006. Soil nitrogen availability in tallgrass prairie under the fire-grazing interaction. Rangeland Ecology & Management 59:625–631.

Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate, or CO_2? Climatic Change 29:91–99.

Archibald, S., W. J. Bond, W. D. Stock, and D. H. K. Fairbanks. 2005. Shaping the landscape: fire-grazer interactions in an African savanna. Ecological Applications 15:96–109.

Augustine, D. 2010. Spatial versus temporal variation in precipitation in a semiarid ecosystem. Landscape Ecology 25:913–925.

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165–1183.

Axelrod, D. I. 1985. Rise of the grassland biome, central North-America. Botanical Review 51:163–201.

Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49:386–400.

Bates, D., and M. Maechler. 2010. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-33. ⟨http://CRAN.R-project.org/package=lme4⟩

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419–431.

Belsky, A. J., and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. Conservation Biology 11:315–327.

Bowyer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity & Distributions 12:244–257.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Briggs, J. M., G. A. Hoch, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586.

Brock, F. V., K. C. Crawford, R. L. Elliott, G. W. Cuperus, S. J. Stadler, H. L. Johnson, and M. D. Eilts. 1995. The Oklahoma Mesonet: a technical overview. Journal of Atmospheric and Oceanic Technology 12:5–19.

Brockway, D., R. Gatewood, and R. Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. Journal of Environmental Management 65:135–152.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, USA.

Burns, C., S. Collins, and M. Smith. 2009. Plant community response to loss of large herbivores: comparing consequences in a South African and a North American grassland. Biodiversity and Conservation 18:2327–2342.

Clary, W. P. 1995. Vegetation and soil responses to grazing simulation on riparian meadows. Journal of Range Management 48:18–25.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747.

Coppedge, B. R., D. M. Engle, C. S. Toepfer, and J. H. Shaw. 1998. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. Plant Ecology 139:235–246.

Coppock, D. L., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. Oecologia 56:10–15.

Cummings, D. C., S. D. Fuhlendorf, and D. M. Engle. 2007. Is altering grazing selectivity of invasive forage species with patch burning more effective than herbicide treatments? Rangeland Ecology & Management 60:253–260.

du Toit, J., and D. Cumming. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. Biodiversity and Conservation 8:1643–1661.

Engle, D. M., S. D. Fuhlendorf, A. Roper, and D. M. Leslie. 2008. Invertebrate community response to a shifting mosaic of habitat. Rangeland Ecology & Management 61:55–62.

Fritz, K. M., W. K. Dodds, and J. Pontius. 1999. The effects of bison crossings on the macroinvertebrate community in a tallgrass prairie stream. American Midland Naturalist 141:253–265.

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604–614.

Fuhlendorf, S. D., D. Engle, J. D. Kerby, and R. G. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conservation Biology 23:588–598.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gordon, I. J., A. J. Hester, and A. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

Hamilton, R. G. 2007. Restoring heterogeneity on the Tallgrass Prairie Preserve: applying the fire–grazing interaction model. Pages 163–169 *in* Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems. Tallahassee, Florida, USA.

Hartnett, D. C., A. A. Steuter, and K. R. Hickman. 1997. Comparative ecology of native and introduce ungulates. Pages 72–101 *in* Ecology and conservation of Great Plains vertebrates. Springer, New York, USA.

Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecological Applications 4:461.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Holland, J., D. Bert, and L. Fahrig. 2004. Determining the spatial scale of species' response to habitat. Bioscience 54:227–233.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven.

Jacobs, J. 1974. Quantitative measurement of food selection: a modification of forage ratio and Ivlev's electivity index. Oecologia 14:413–417.

Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications... a review. Journal of

Range Management 37:430–438.

Kauffman, J. B., W. C. Krueger, and M. Vavra. 1983. Effects of late season cattle grazing on riparian plant communities. Journal of Range Management 36:685–691.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. Bioscience 49:39–50.

Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins. 1998. Grassland dynamics : long-term ecological research in tallgrass prairie. Oxford University Press, New York, USA.

Leonard, S., J. Kirkpatrick, and J. Marsden-Smedley. 2010. Variation in the effects of vertebrate grazing on fire potential between grassland structural types. Journal of Applied Ecology 47:876–883.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Lott, D. F. 2002. American bison: a natural history. University of California Press, Berkeley.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. Erickson. 2002. Resource selection by animals: Statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht.

Manning, R. 1995. Grassland : the history, biology, politics, and promise of the American prairie. Viking, New York, USA.

McAllister, R., I. Gordon, M. Janssen, and N. Abel. 2006. Pastoralists' responses to variation of rangeland resources in time and space. Ecological Applications 16:572–583.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist 132:87–106.

Milner, J., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:36–47.

National Park Service. 2009. Tallgrass Prairie National Preserve, Kansas, bison management plan, environmental assessment. National Park Service, United States Department of Interior.

Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecological Applications 3:631–643.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨http://www.R-project.org⟩

Revolution Computing. 2009. foreach: Foreach looping construct for R. R package version 1.3.0. ⟨http://CRAN.R-project.org/package=foreach⟩

Reynolds, H., C. Gates, and R. Glaholt. 2003. Bison. Pages 1009–1060 *in* Wild mammals of North America: biology, management, and conservation. Johns Hopkins University Press, Baltimore.

Ripple, W., and R. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184:299–313.

Rook, A. J., B. Dumont, J. Isselstein, K. Osoro, M. F. WallisDeVries, G. Parente, and J. Mills. 2004. Matching type of livestock to desired biodiversity outcomes in pastures - a review. Biological Conservation 119:137–150.

Samson, F. B., and F. L. Knopf. 1994. Prairie conservation in North America. Bioscience 44:418–421.

Sanderson, E. W., K. H. Redford, B. Weber, K. Aune, D. Baldes, J. Berger, D. Carter, C. Curtin, J. Derr, S. Dobrott, E. Fearn, C. Fleener, S. Forrest, C. Gerlach, C. Gates, J. E. Gross, P. Gogan, S. Grassel, J. A. Hilty, M. Jensen, K. Kunkel, D. Lammers, R. List, K. Minkowski, T. Olson, C. Pague, P. B. Robertson, and B. Stephensom. 2008. The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. Conservation Biology 22:252–266.

Schepers, J., and D. Francis. 1982. Chemical water-quality of runoff from grazing land in Nebraska. 1. Influence of grazing livestock. Journal of Environmental Quality 11:351–354.

Searle, K. R., L. P. Hunt, and I. J. Gordon. 2010. Individualistic herds: individual variation in herbivore foraging behavior and application to rangeland management. Applied Animal Behaviour Science 122:1–12.

Sensenig, R. L., M. W. Demment, and E. A. Laca. 2010. Allometric scaling predicts preferences for burned patches in a guild of East African grazers. Ecology 91:2898–2907.

Sheldon, B., and S. West. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. American Naturalist 163:40–54.

Steuter, A. A., and L. Hidinger. 1999. Comparative ecology of bison and cattle on mixed-grass prairie. Great Plains Research 9:329–342.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92.

Towne, E. G., D. C. Hartnett, and R. C. Cochran. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. Ecological Applications 15:1550–1559.

Trimble, S. W., and A. C. Mendel. 1995. The cow as a geomorphic agent - a critical review. Geomorphology 13:233–253.

VanWagoner, H. C., D. W. Bailey, D. D. Kress, D. C.

Anderson, and K. C. Davis. 2006. Differences among beef sire breeds and relationships between terrain use and performance when daughters graze foothill rangelands as cows. Applied Animal Behaviour Science 97:105–121.

Vermeire, L. T., R. B. Mitchell, S. D. Fuhlendorf, and R. L. Gillen. 2004. Patch burning effects on grazing distribution. Journal of Range Management 57:248–252.

Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. American Midland Naturalist 129:10–18.

van Vuren, D. 1982. Comparative ecology of bison and cattle in the Henry Mountains, Utah. Pages 449–457 *in* Wildlife-Livestock Relationships Symposium held at Coeur d'Alene, Idaho, April 20–22, 1981. Forest, Wildlife & Range Experiment Station, University of Idaho, USA.

Weston, S. 2009. doMPI: Foreach parallel adaptor for the Rmpi package. R package version 0.1-4. ⟨http://CRAN.R-project.org/package=doMPI⟩

Wilsey, B. J. 1996. Variation in use of green flushes following burns among African ungulate species: the importance of body size. African Journal of Ecology 34:32–38.

With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation 141:3152–3167.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology, United States and southern Canada. Wiley, New York, USA.

Yu, H. 2010. Rmpi: Interface (wrapper) to MPI (Message-Passing Interface). R package version 0.5-8 ⟨http://CRAN.R-project.org/package=Rmpi⟩

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Creating a reserve within the Thunder Basin National Grasslands

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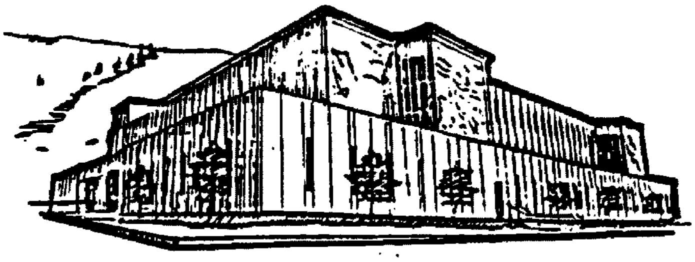

Creating a Reserve within the Thunder Basin National Grasslands

by

Elizabeth Gaines

B. A. Colorado College, 1990

presented in partial fulfillment of the requirements

for the degree of

Master of Science

The University of Montana

1996

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MARCH 7, 1996

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Creating a Reserve within the Thunder Basin National Grasslands

Committee Chair: Len Broberg

This professional paper addresses the obstacles that prohibit the Thunder Basin National Grasslands of northeastern Wyoming from functioning as an ecosystem. By using the Thunder Basin National Grasslands as a model, aspects of conservation biology, economics, law, federal management practices, public land consolidation and land use reform are considered to develop a series of steps toward ecological recovery.

This examination of present conditions of the Wyoming prairie ecosystem and the series of strategies suggested for prairie recovery and preservation are meant to be universally applicable to the American Northern Plains. This paper should function as a guide for advocates and concerned individuals interested in identifying and protecting contiguous pieces of public land in the Northern Plains. Livestock grazing, roads, federal management bias and land fragmentation are discussed as current obstacles that prevent a pristine prairie ecosystem.

The recommendations presented in this paper enable the hypothetical creation of an ecological reserve within the scattered pieces of public land in Thunder Basin National Grasslands. Grassland species re-introduction, recovery efforts and recreation possibilities are presented as ecologically sound alternatives to livestock grazing and other forms of resource extraction in northeastern Wyoming.

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Foreword

[The Great Plains] are wholly unfit for cultivation, and of course uninhabitable by a people depending on agriculture for their substance. Although tracts of fertile land considerably extensive are occasionally to be met with, yet the scarcity of wood and water, almost uniformly prevalent, will prove an insuperable obstacle in the way of settling this country. This is a region that seems particularly adapted to buffaloes, wild goats and other wild game; incalculable multitudes of which find ample pasturage and subsistence upon it.

(Explorer Maj. US Long, 1820)

In an effort to address the diminishing biodiversity of the Northern Plains, this paper details a series of recommendations for prairie protection. Using the Thunder Basin National Grasslands (TBNG) as a model, I will show that federal management must implement biological, legal and political remedies to protect Northern Plains regions. TBNG is an ideal study area because it provides examples of almost every problem conflicting with ecological integrity in the mixed grass prairie ecosystem on Great Plains public lands. This paper is meant to function as a guidebook. Although the following chapters tailor solutions to TBNG, the suggestions can be universally applied to the High Plains region.

The project fits into a larger effort in High Plains protection, the High Plains Ecosystem Recovery Plan (HPERP). The goal of HPERP is to identify large tracks of federal land within the High Plains region, link these lands with corridors, and create a contiguous block of public land adequate for the maintenance and re-introduction of minimum viable populations of prairie species. HPERP looks to include sections of Bureau of Land Management (BLM) lands; state lands; Native American reservation lands; National Grasslands and US Forest Service (USFS) lands; nature preserves; conservation easements; Wild and Scenic River corridors; and other suitable lands in the plains bioregion throughout Montana, Wyoming, North and South Dakota, Nebraska and Colorado.

HPERP is particularly timely. According to the socio-economic studies of sociologists, (Popper 1991) human communities within the Great Plains are currently facing an acute economic slump. Despite mining and grazing in this region, community economies in the Great Plains do not register significant earnings on a national economic grid, indicating that existing extractive industries do not support High Plains communities (Popper, 1991). So as national economics of the plains states continue to force a human depopulation trend (Popper, 1991), some original biodiversity may soon have the opportunity to reclaim former habitat.

The reality that the biosphere is driven by.....interdependence...challenges both small minds and big governments. (Judy Meyer and Gene Helfman)

Introduction

Grasslands--Going, going, gone

Men of every rank were eager to get into the cow business. In a short time every acre of grass was stocked beyond its fullest capacity. Thousands of cattle and sheep were crowded on the ranges when half the number were too many. The grasses were entirely consumed; their very roots were trampled into the dust and destroyed. In their eagerness to get something for nothing speculators did not hesitate at the permanent injury, if not the total ruin, of the finest grazing country in America.

(H.L. Bentley, 1898, somewhere on the American Plains)

The plains stretch from the Rocky Mountains eastward to meet the tallgrass prairies of Illinois, Kansas and Oklahoma. Southern prairie extends into Northern Mexico and the northern prairie extends into Canada (Brown, 1989). The northern grasslands, or High Plains, refer to shortgrass prairies that still cover much of eastern Montana, eastern and southern Wyoming, North and South Dakota, eastern Colorado and parts of Nebraska. The existing natural prairie regions of these North American states, however, are simply a small remnant of its historic extent.

A hundred years of pressure from ranching, farming and mining have damaged this ecosystem, wiping out most of the once prolific biodiversity. Without a strategy to preserve the remaining biota of the shortgrass prairie, the Northern Plains will continue to deteriorate, leaving only a giant livestock pasture.

Human impacts have resulted in significant damage to both wildlife species as well as vegetation. The coming of Europeans to the western United States created a tradition of homesteading, sodbusting and ranching , decimating the prairie's rich mosaic of grasses. As bison were wiped out, cattle and sheep overtook the grasslands. Monocultures of alfalfa, winter wheat, and crested wheatgrass, edged out many native climax species (Davis, 1994). Native species such as buffalo grass, blue grama, hairy grass, and large leaf sage were also replaced with low grade, invader species as a result of prairie deterioration (Brown, 1989).

Early in the century, in the effort to protect their defenseless livestock herds, many ranchers targeted and exterminated the plains grizzly and gray wolf from the plains. Of the large predators, only the mountain lion and the coyote still remain in the High Plains. Prairie dogs, thought to compete with livestock for forage, were also marked for extinction. Prairie dog extirpation programs, regional shooting programs, farming practices and conversion of grasslands facilitated staggering declines in prairie dog populations. (Carlton, 1994)

The prairie dog was recently petitioned by the Biodiversity Legal Foundation for endangered species listing (Carlton, 1994). Because the Black-tailed (*Cynomys ludovicianus*) and White-tailed (*Cynomys leucarus*) prairie dogs provide food and habitat (burrow) to as many as 164 associated species, as prairie dog colonies declined, many other dependent species populations followed. Some of the species adversely effected include the ferruginous hawk (*Buteo regalis*), the mountain plover (*Charadrius montanus),* the burrowing owl (*Speotyto cunicularia*) and listed endangered species, the swift fox (*Vulpes velox*) and the black-footed ferret (*Mustela nigripes*) (BLF, 1994). Species no longer found on the plains are the gray wolf (*Canis lupis),* bison (*Bison bison*) and the grizzly bear (*Ursus acrtos horribilis*).[1]

Like the entire shortgrass prairie ecosystem, the ecological state of the TBNG is degraded. Moreover, there are no current federal efforts for management reform or biotic recovery. Although TBNG has been mentioned as a re-introduction site for the black-footed ferret and bison (USFS, 1986), obstacles continue in this grassland which may prevent the survival of the ferret, bison and many other prairie species.

As it stands, the Northern prairie is in need of rescue. Although the first step to plains recovery will be to identify and challenge detrimental cultural practices, implementation of many suggestions will require legal, legislative and community outreach for successful implementation. [2]

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[1] The Black-footed ferret is being re-intoduced to some plains regions.

[2] Outreach is essential and tricky. Community work will not be discussed in this document, but is none the less an important part of reform.

Methodology for Ecosystem Reconstruction

The northern plains of Wyoming have been targeted for intention of protection and assimilation into HPERP. The following methodology should be used as a guideline.

1) Select a region within the plains bioregion containing large sections of federal land acreage:
   - determine land ownership (federal, state, private)
   - assess patterns of mixed ownership

2) Study current uses of land
   - determine livestock numbers
   - determine mining operations
   - study files on range conditions and ranching operations

3) Study the health of the region
   - determine sensitive plant and animal species in the area
   - determine native species that are missing
   - critique federal management monitoring program for sensitive species' critical habitat, riparian areas, ecosystem integrity

4) Identify obstacles for intact ecosystems
   - determine how livestock grazing presents problems for the ecosystem
   - determine how human manipulation of the range presents ecological problems
   - examine mining efforts within the ecosystem
   - examine land fragmentation effects on ecosystem integrity

5) Classify current management practices for the region
   - examine how management creates; perpetuates; removes obstacles

preventing a complete intact prairie
- determine if management decisions include looking at the effects on all species in the ecosystem
- determine if management decisions are made with thought toward restoration and future re-introductions

6) Study federal lands and identify key private linkages between federal tracts in the context of establishing contiguous habitat with thought toward bison range and large predator ranges.

7) Consider means for federal protection of the area
- consider legal means to challenge and remove threats to ecosystem integrity
- consider means of land acquisition for linkages and critical habitat
- consider outreach into local communities

8) Consider budget and fund-raising opportunities
- assess expense of strategies and fund-raise for budget
- determine legal expenses and research *pro bono* opportunities
- determine lobbying expenses for legislative routes
- consider restoration expenses and re-introduction expenses
- contact foundations, universities and native species farms and ranches for monetary assistance, volunteer work and donations

9) Identify benefits to the region
- research how change will benefit or harm local economy
- determine if communities will be sustainable despite various subsidy cuts
- show how recreation and tourism will improve economy

10) Suggest implementation of a plan for native prairie ecosystem recovery
- present restoration goals/methods
- secure legal and legislative protection
- restore biodiversity as necessary

With these guidelines in mind, the following text discusses implementation of ecosystem recovery strategies in the TBNG.

Chapter 1

Thunder Basin National Grasslands

It would have been easier to count the leaves in the forest than it would to count the number of buffaloes living at any given time prior to 1870--(**museum curator W.T. Hornaday, 1905**)

Thunder Basin National Grasslands (TBNG), is administered by the Douglas Ranger District of the Medicine Bow National Forest in northeastern Wyoming. Bordered by the Black Hills on the east and by the Bighorn Mountains on the west, the TBNG is located within a topographic depression known as the Powder River Basin. The area contains four separate ecotypes due to variations in elevation, topography and microclimates: upland plains -- a high plateau on the western edge of the TBNG; escarpments -- eroded plains that have formed walls measuring 300-400 feet on the eastern and northeastern edges of TBNG; broken dissected plains -- a series of ridges and plains; and shale uplands -- shaley soils on the Black hills uplift that are typified by ponderosa pine growth. (USFS, 1990) To the southwest of TBNG rises Laramie Peak, a northern peak in the Laramie range.

The climate in TBNG is semi-arid, with summer temperatures exceeding 90 degrees and winter temperatures dropping below -40 degrees. Average annual rainfall is about 11 inches with snowfall constituting 1/3 of the annual precipitation. There are five vegetation types in the TBNG: grassland type -- including western wheatgrass, blue grama, needle and thread; sagebrush/grassland type -- including big sagebrush, blue grama and prickly pear; greasewood/cottonwood type -- including cottonwoods, greasewood, silver sagebrush, western wheatgrass and inland saltgrass; ponderosa pine/juniper type -- including ponderosa and juniper stands with bluebunch wheat grass, blue grama and big sagebrush; and badland type -- including sagebrush, yucca and western wheatgrass. (USFS, 1990)

Resources, Past and Present

Not even a buffalo was now in sight to relieve the dull monotony of the scene; although during some seasons, particularly fall, these prairie's are literally strewn with herds of this animals. (Early traveler to Wyoming, circa 1872)

From the late 1800's to the 1920's, many homesteaders abandoned this portion of Wyoming, finally understanding that the region was "*not suitable for cultivation of cash crops and the homesteads were too small to support successful livestock operations. Early efforts to make the land produce beyond its physical limits resulted in serious depletion of the basic resources of the prairie land--the soil and the grass sod which protected it.""* (USFS, 1994) After the plains dust bowl and the Great Depression many homesteads were abandoned. The Thunder Basin National Grasslands was created by Congress in 1934.

In 1954, these lands were transferred from the Soil Conservation Service to the US Forest Service for management. There are currently 267 grazing allotments and 231 separate grazing permittees, accommodating 177,400 Animal Unit Months (AUM's) yearly[3]. (USFS 1990) The average size of a ranch operation (private and public lands combined) is 8,000 acres.

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[3] The equivalent of 160,500 animal units per month in the Thunder Basin and 16,900 in the Laramie Peak region.

(USFS 1990) TBNG accommodates 24,000 head of cattle and 21,000 head of sheep, and 3,200 miles of road (USFS 1990). Currently every acre is leased for mining, presently including 450 oil and gas wells, 5 coal strip mines, numerous deposits of uranium, an operating uranium mine, and 33 abandoned bentonite mines (USFS 1990).

Industry in TBNG

Like a majority of the public lands in the Northern plains, TBNG is a jumble of public lands and private inholdings (See Figure 1 ; **Thunder Basin National Grasslands,** p. 10) that encompasses 1,799,918 acres through eight counties.[4] It boasts one of the largest single ranger districts in the country, the Douglas Ranger District in Douglas, Wyoming (USFS, 1990). Private inholdings in TBNG comprise 56% of the region. Currently the region is divided into three grazing associations: Spring Creek Association in northern Cook and Campbell counties; Inyan Kara Association in Weston and Niobrara counties, and the Thunder Basin Association in Converse, southern Campbell and Weston counties. Over 188,500 Animal Unit Monthly are permitted yearly in the TBNG.

Thunder Basin National Grasslands experiences many ecological, political and cultural situations that seem to typify the northern grasslands. At present, the management and land distribution in the TBNG is not adequate to support a healthy, naturally functioning grassland ecosystem.

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[4] TBNG extends 92 miles east and west and 192 miles north and south. The total number of USFS acres is 1,799,918 within TBNG. Private acres total 1,114,348 acres. State lands total 133,346 acres.

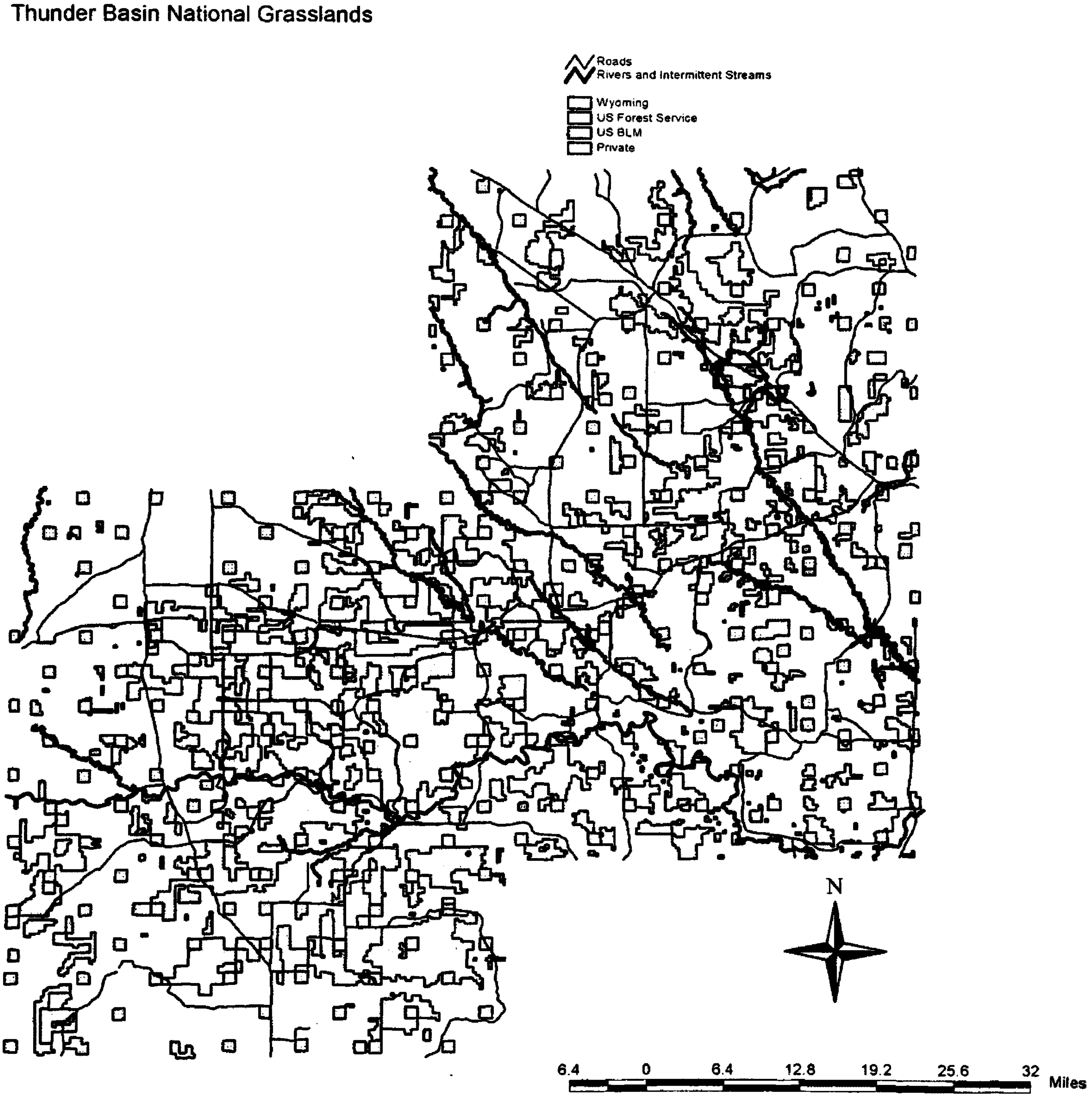

Figure 1. Thunder Basin National Grasslands ownership patterns.

Without restoration, this area would make a poor candidate for bison and ferret re-introduction [5]. Wildlife takes a back seat to livestock in management considerations.

Despite the proven historic inability for this region to sustain large ranching and farming efforts, ranching is the central use of TBNG and management focus. The area is managed almost completely for its commodity resources with little thought given to its ecological limits, attributes, or threatened or endangered species. Grazing allotments are not monitored and many allotments have no Allotment Management Plans (AMP'S).[6] In short, the grazing policies implemented by the USFS in TBNG are completely inconsistent with a healthy, diverse ecosystem or the productive capabilities of the area. USFS management's favoritism and short-sightedness prohibits TBNG from being both ecologically sound and recreation oriented.[7]

Replacing Biodiversity with Livestock

> *The proposed plan calls for grazing 245,000 AUM's per year to 250,000 in the next 10 years. Livestock management during the next 10 years would allow recovery of rangelands that are currently in less than satisfactory condition by redistributing grazing use to areas that are underutilized.*
> **(Medicine Bow Resource Management Plan for the Thunder Basin, 1985)**

Thunder Basin has thousands of cattle and sheep (250,000 Animal Unit Months) that graze habitat formerly occupied by the American bison.

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[5] Thunder Basin National Grasslands has been recommended for a possible site for black-footed ferret re-introduction and bison re-introduction. (USFS, 1989)

[6] At present over 70 allotments at TBNG lack AMP'S. AMP's over ten years old total over 36.

[7] There are no campgrounds on the the grasslands, although there are four on Laramie Peak.

Native grazers, such as pronghorn, antelope, and deer[8] are still prevalent in TBNG and continue to graze along with cattle; but for the bison, millions of prairie dogs, black footed ferrets, wolves, grizzly bears, and natural grass communities, a hundred years of agriculture and mining in the TBNG have caused extinctions and declines in populations of many native species. (USFS, 1992) Presently, the following species in TBNG are identified as threatened, according to a 1992 USFS inventory:

Fish

Flathead Chub, (Hybopsis gracilis) found in Antelope Creek, the Cheyenne River, and the Little Powder River
Plains Topminnow, (Fundulus scaiadicus) , found in North and South Platte drainages, the Niobrara river and the headwaters of the Cheyenne River system.

Reptiles

Milk Snake, (Lampropeltis trianqulum) , found in prairie systems, broadleaf riverbottoms and under decaying wood.
Black Hills Red Bellied Snake, (Storeria occipitomeoculae pahasapae) , found in the Upton/Osage area.

Amphibians

Tiger Salamander , (Ambystoma tigrinum) found in intermittent streams and stock ponds.
Northern Leopard Frog , (Rana pipiens) found on pond and lake shores in cattails, sedges and tall grasses.

Mammals

Townsend Big Earred Bat, (Plecotus townsendii) found in Upton-Osage region.

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[8] There are opposing studies on whether cattle compete with prairie antelope, deer and elk for forage. (Jacobs, 1991 and TBNG study USFS, 1990)

Fringed-tailed Myotis , (Myotis thysanodes pahasapensis) found in Weston, Cow Creek and Downs areas.
Swift Fox , (Vulpes velox) still found in upland habitats of TBNG.

Birds

American Bittern, (Botaurus lentiginosus) summer resident very rare in TBNG. Found in riparian areas
Western Yellow Billed Cuckoo, (Coccyzus americanus) found in riparian areas.
Greater Sandhill Crane, (Grus canadensis) found in wetlands.
Long-Billed Curlew , (Numenius americanus) found in sagebrush and grassland types.
Ferruginous Hawk , (Buteo regalis) found in grasslands--ground nesters.
White-faced Ibis , (Plegadis chihi) found in the wetlands on the grasslands.
Common Loon , (Gavia immer) found along river banks.
Merlin, (Falco columbarius) found in cottonwood river bottoms throughout the year.
Western Burrowing Owl , (Athene culumbarius) found in vacant prairie dog burrows on the grasslands.
Loggerhead Shrike , (Laniuius ludovicianus) found upland sagebrush and grasslands.
Fox Sparrow ,(Passerella iliaca) found in riparian shrublands.
Black Billed Woodpecker , (Picoides acrticus) found mainly in burned forests.
Mountain Plover , (Charadrius montanus) found on grasslands with level topography and short grasses; prairie dog towns.
Upland Sandpiper , (Bartramia longicauda) found on grasslands.
Baird's Sparrow , (Ammodramus bairdii) found nesting on ground in grasslands.
Black Tern , (Chlidonias niger) found in riparian regions.
Lewis Woodpecker (Melanerpes lewis) found on cottonwood bottoms and in ponderosa pine stands.
(USFS, 1992)

According to a 1991 USFS survey, pronghorn antelope populations total 54,307; mule deer populations total 26,900; white-tailed deer populations total 1,651; elk populations total 2,404; big-horned sheep total 212 and 12 moose (in the Laramie Peak region) (USFS, 1992). Prairie dog towns cover 13,000 acres, although a recent sylvatic plague outbreak has wiped out a significant number of rodents within Thunder Basin and exact prairie dog population numbers are unknown (USFS, 1995). Predators include black bear, bobcat, coyote, raccoon, skunk, mountain lion, ermine, badger, long-tailed weasel, red fox, and swift fox. No black-footed ferrets have been found in this region since the 1970's.[9]

TBNG presently provides habitat for over 228 bird species (60 neotropical species), including ferruginous hawks, peregrine falcons, burrowing owls, and mountain plovers as well as 62 mammals, 15 reptiles, 28 fish and 6 amphibian species (USFS 1990). Bald eagles and Golden Eagles nest in TBNG. The TBNG has a variety of habitats: old growth ponderosa pine stands, shrub and sagelands, scoria outcroppings, marshes, river bottoms, cottonwood stands, and shortgrass plains supporting 22 different plant communities inhabited by 250 species of vascular plants. The rivers in TBNG include the Little Powder, Little Missouri, Bell Fourche and the Cheyenne River (USFS, 1992).

Grazing and so-called grazing improvements have been a significant ecological and financial burden to the High Plains. Cattle management includes pest elimination programs (coyote and prairie dog management); fire-suppression, a practice that prevents vegetation communities from

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[9] A population of black-footed ferrets was discovered in 1982 on a ranch in Shirley Basin, about 100 miles west of TBNG

reaping fire's healthy benefits; fencing and barbed wire; and roads (Ferguson and Ferguson, 1983).

"Pest" control, a component of the TBNG grazing pragram, has been responsible for reducing prairie dog range 98% (Clark, 1989). Between 1982 and 1992, Federal and State governments have been responsible for poisoning 1,193,203 acres of prairie dog habitat, and despite shrinking prairie dog populations, control programs continue at the TBNG full speed ahead (USFS, 1989). From 1989 to 1992, over $388,700 was spent on prairie dog control programs on state, private and federal lands in Wyoming (Forrest and Roemer, 1993). Indirect costs for grain and aluminum phosphate totaled over $50,000 (Forrest and Roemer, 1993). Most of the funds went to Campbell County, the Medicine Bow National Forest and TBNG (Forrest and Roemer, 1993).

Predator control for ranching operations has been responsible for the innumerable deaths of coyotes, mountain lions, bobcats, bald and golden eagles (Jacobs 1991). Control programs have also been responsible for wiping out the wolf, swift fox, black bear and grizzly from the plains region (Jacobs 1991). Animal Damage Control (ADC) uses aerial hunting, traps, snares and carbon monoxide poisoning on coyotes in TBNG (USDA, ADC, 1993).

Although the black-footed ferret is currently being re-introduced to areas in Montana and Wyoming, the ferrets have a low probability of attaining a viable population if not enough effort is made to protect the prairie dog (Forrest, 1993). Ferret populations declined originally due to lack of prey base (99% of their diet are prairie dogs) and diminishing habitat.[10] Without a healthy population of prairie dogs, 10-30 per hectare (O'Mielia, 1980), black-footed ferrets will not find a suitable prey base if re-introduced to TBNG.

Grazing and Vegetation

> *Native annuals have been greatly depleted and even extirpated by from many areas* [in the Plains] *by grazing. Over even greater areas, ranching's "desertifying" effects have eliminated perennial ground cover and created conditions favorable to annuals--exotic annuals.* (Jacobs, 1991)

The vegetation in the plains has also been altered due to cattle grazing. The rarest grasses on the grasslands are generally the most sought after by livestock (Jacobs, 1991). Undesirable species and exotics come in after the native species are eaten, causing shifts in vegetation patterns.[11] Bare soil, an effect of over-grazing, allows erosion, floods, and prevents proper moisture absorption by the soils. Riparian areas, rare and vital parts of the prairie, are damaged by cattle trampling stream banks and sensitive vegetation, such as cottonwoods and sedges. Reduction in streamside vegetation makes flash floods a real danger through erosion and the destablization of streambanks (Jacobs, 1991).

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[11] Cheatgrass, an invader common in TBNG, followed cattle into the plains around the turn of the century. It is an inferior grass to native grass and causes injury to livestock by lodging in soft animal tissues. (Jacobs, 1991)

Mining

Extensive oil and gas field development has occurred on state and private land, as well as on federal... The character of the entire area is heavily influenced by oil and gas development, such as oil rigs, pumpjacks, storage, treater tanks, pipelines, power lines and oilfield roads and traffic.
(TBNG USFS overview, 1990)

The Forest Service has opened up 100% of the Thunder Basin National Grassland to oil and gas leasing, and ten new wells are developed annually. TBNG has 58 developed oil fields with 1,500 wells[12], and each field is accessed by its own road and pipeline system. The Forest Service reports that coal underlies a majority of the Thunder Basin region: "thousands of acres of coal deposits with a high to moderate potential for development" exist (USFS, 1990). At this point, five coal mines operate on 3,700 acres of public land. Annually, the mines produce 55,000,000 tons of coal. Presently, oil, gas and mineral revenues exceed $27 million in annual profit (USFS, 1990) .

There are two operating bentonite mines in the Thunder Basin. Since the price of bentonite is down, however, mining activity is low. Bentonite mining has gone through lucrative spurts and currently 33 abandoned bentonite mines are left awaiting reclamation funding (USFS, 1990). Only one uranium mine exists on TBNG, although there are many other abandoned uranium mines. Sand, gravel and building stone are currently mined on TBNG. Hard rock mining experienced a boom at the turn of the century on Laramie Peak, however today only one prospecting operation

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[12] Only 400 wells on the Thunder Basin are producing wells.

exists. "Old claims" on Laramie Peak are under analysis for hazard mitigation and reclamation work (USFS, 1990).

There are no areas within TBNG that are off limits to mining. Riparian and wetland areas; steep slopes; unstable soils; raptor and grouse nesting sites are all subject to unmitigated mining disturbance (Keopsel, 1992). Road building, erosion of unreclaimed mining sites and excavation are documented causes of watershed siltation, water contamination, and destruction of habitat and vegetation patterns in riparian areas (Smith, 1995). Mining is a danger to water quality in TBNG (Keopsel, 1992).

Ownership Patterns

The TBNG is a mixture of state, BLM, USFS and private lands (see Figure 1; **Thunder Basin National Grasslands**, p. 10). Homesteading saw the rise of sod busting on the plains, but when the wheat price peaked and plummeted in the early 1930's, two and a half million people abandoned their dryland farms. The acreage of these homesteads reverted back to federal land with the creation of the Bankhead-Jones Farm Tenant Act. This accounts for the checkerboard pattern, or blocks of federal land interspersed with private inholdings throughout the plains. On TBNG, only 44% of the lands are public, and the remaining 56% are private inholdings (USFS, 1990).

Chapter 2

Conservation Biology and Ecosystem Recovery

Conservation biology is "the application of science to conservation problems, addressing the biology of species, communities, and ecosystems that are disturbed, either directly or indirectly, by human activities and other agents" (Cooperrider, 1994). As it stands, USFS management in TBNG overwhelmingly favors resource development to the exclusion of conservation biology principles and biodiversity.[13] Management direction at the Douglas Ranger District lacks conservation aims essential to grassland recovery. In order to address the conservation problems in TBNG and restore the natural systems of the prairie ecosystem, conservation biology needs to enter management, practice and philosophy. The following excerpts outline the difference between the conservation planning criteria in the Medicine Bow Grasslands Resource Management Plan (RMP) and Noss and Cooperrider's (1994) criteria for conservation planning in *Saving Nature's Legacy ; Protecting and Restoring Biodiversity* .

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[13] According to the "USFS Rules of Management for Thunder Basin National Grasslands Grazing Associations", TBNG objectives call for "progressive principles of land conservation and multiple use, the development of grassland agriculture and sustained-yield management of the range resources within the Association. " USFS goals call to " demonstrate livestock grazing associated with other uses in a way, that when practiced on these lands, will provide the greatest return from the investment in multiple use management and the best use of all lands in the area. " There is no use of the term biodiversity or ecosystem in the entire document.

RMP (USFS, 1985)

1) Promote and develop grassland agriculture and sustained yield management of the fish and wildlife, timber, water, and recreation resources in the area.
2) Demonstrate sound and practical land uses for the area.
3) To the extent feasible, integrate federally owned land with the associated private lands into natural management units which favorably influence development of sound land conservation and and utilization practices suitable for use in the area.
4) Provide a biological benchmark in man's quest to live harmoniously with extremes of climate, land and economic fluctuations.
5) Serve as an applied range management laboratory testing the latest techniques in grassland agriculture and determining sound land management and sustained production.
6) Provide for rural development and economic and social stability of local communities.

SNL (Noss and Copperrider, 1994)

1)Maintain viable populations of all native species
2) Represent within protected areas, all native ecosystem types across their natural range of variation.
3) Maintain evolutionary and ecological processes (i.e., disturbance, regimes, hydrological processes)
4) Manage over periods of time long enough to maintain the evolutionary potential of species and ecosystems
5) Accommodate human use and occupancy within the above mentioned constrains.

Comparing the above priorities, it is easy to see that the USFS is more committed to resource extraction in the TBNG than to the ecological integrity of the ecosystem. The conservation biologists frame their goals within a holistic structure, allowing human use only if it meets the goals of the above mentioned criteria (#5, SNL) for a healthy environment. The RMP looks at TBNG as an "agricultural laboratory"(#5, RMP), or a "benchmark" set up to accommodate human use despite the ecology, topography and climate (#4,6, RMP) of the TBNG. Before management specifics are addressed within the Thunder Basin region, a shift in management philosophy is essential. If the area is to accommodate native species such as the black-footed ferret, swift fox or bison, TBNG needs to be perceived as a prairie ecosystem (Forrest, 1994) rather than a "laboratory for the latest techniques in grassland agriculture."

Although the Medicine Bow National Forest and Thunder Basin Resource Management Plan addresses "wildlife", the management goals focus on game species and not the many other members of the region's biotic community. Resource managers manage game species and livestock, but fail to address non-game species, many of which aren't even studied. (Alverson et. al, 1994) This approach leaves out key ecosystem components and prevents a holistic approach to resource management and ecosystem integrity.

Conservation Biology and the Noss Model

Wilderness recovery , I firmly believe, is the most important task of our generation

(Reed Noss, 1992)

Biodiversity

Reed Noss, a conservation biologist and the Science Editor for *Wild Earth,* explains that implementation of conservation principles requires large pieces of contiguous roadless habitat to support genetic variability, to withstand environmental disruptions (disease, fire, weather patterns) and to promote evolutionary potential with a long-term vision (Noss, 1992). Land pieces need to be connected by a network of corridors to form interconnected core reserves that allow for genetic cross-over. With this model in mind, large blocks of habitat first need to be identified within the TBNG, and then acquired, connected and protected.

To cobble together an ecosystem protection plan, TBNG must first consolidate federal lands and if need be, private lands. Acquisition of private lands that connect public pieces to create a contiguous reserve,[14] should be an essential goal in the TBNG Resource Management Plan in order to accommodate large predators, bison, and prairie diversity. At present, the TBNG Land Swap Program is available to local landowners who want to buy or trade for public lands. The program is for ranching and the concept of seeking and acquiring lands of ecological importance is not a component of the program. If contiguous habitat is to be achieved, a strategy could be to shift the Land Swap Program focus from "ranch real estate" to "conservation real estate."

Noss suggests the following guidelines for management goals subsequent to establishment to core habitat:

* Maintain minimum viable populations well distributed across native ranges
* Maintain large blocks of habitat for target species
* Habitat blocks should be close together
* Habitat should be contiguous
* Corridors should connect habitat blocks
* Blocks of habitat should be roadless[15]

Wildlife includes all species living in the prairie biotic community, even species perceived as pests. A focus on the minimum viable

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[14] Contiguous habitat is essential in preventing isolated populations and weak genetic pools. (Noss, 1992)

[15] According to Steve Forrest, Ph.D., roadless area for the prairie species community may not be as important as it is to the forest species community.

population[16] numbers of prairie dogs should be every bit as important in USFS management goals for the TBNG as pronghorn, deer and elk numbers. Prairie dog communities provide habitat for 164 species (Carlson, 1995) but due to fragmented habitat, disease and an active prairie dog extermination program, prairie dogs are declining at a dangerous rate taking dependent species with them.[17] Carnivores should also be a primary target species for protection and the health of mountain lions, bobcats, and badgers needs to be part of USFS management goals. By assuring minimum viable populations of all species on TBNG, an entire community is accounted for.

Monitoring

One glaring problem in the management of TBNG is the complete lack of routine species monitoring. Although vague references are made in the RMP, transect studies on vegetation on TBNG are intermittent, incomplete, and outdated[18]. Entire regions are overlooked and unknown. A common form of monitoring in TBNG allotment files is the "ocular exam", a drive-by glance of a fence or stock pond. Remarks on inventory sheets are typically, "looks good! not overstocked, etc........" This is not a measurable, accurate form of monitoring. To understand the region and the biota, gap analysis[19] is necessary. Geographic Information System (GIS) integration of a full species

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[16] A viable population is a population with a high probibilty of survival, which according to Noss is 95% or 99%, probability of population persistence for 100 to 1,000 years.

[17] Concerns about population viability should be directed toward species at most risk of extinction in a region. (Noss, 1992)

[18] Many allotments have transect studies dating back to the 1960's.

[19] Gap analysis is a measurement of different community types and species representation within an ecosystem (Noss, 1992). Currently the US Fish and Wildlife is conducting gap on a state wide basis.

inventory, and ground-truthing is also desperately needed. Monitoring needs to be "consistent and scientific."

The following monitoring suggestions are taken from the "Scientific Round Table on Biological Diversity," (Crow et al 1993). The remarks that follow the italicized suggestions may be ecologically beneficial to a new management plan for TBNG:

1) Inventory and monitoring efforts should be expanded and systematized to place them on the best scientific footing to ensure a continual yield of high-quality and timely information.

TBNG- Monitor TBNG on a rotation basis so that each 50 acre by 50 acre section gets assessed every five years.

2)*Research and monitoring should employ the best contemporary science knowledge and methodology. To ensure this process, programs should undergo under peer review.*

TBNG- **Visual or ocular examination, common in allotment files, is not a scientific method of monitoring.** USFS should consult with range biologists and conservation scientists specializing in prairie ecology and begin to use GIS and gap analysis, followed by ground-truthing, to review the prairie ecosystem.

3) Research and monitoring should emphasize those elements of diversity thought to be vulnerable to extirpation, sensitive to man-made disturbances, or keystone species with cascading effects on other elements of diversity.

TBNG- **Shift the research focus from forage for livestock towards the needs of native species within the grasslands ecosystem! This will serve to address the dwindling biodiversity on the TBNG. Studies should focus on**

mountain lion and swift fox populations; riparian health; ferruginous hawks; prairie dogs and plague; and finding native grasses and natural vegetative grasses among degraded prairie.

4) Inventory and monitoring should be extended to include other important but obscure groups of organisms.

TBNG- So little is known of invertebrates in the grasslands. Studies are in order to understand the entire biotic complex.

5) Whenever possible use demographic structure or other early warning signs to assess changed ecological conditions rather than population numbers.

TBNG- Models on weather patterns, disease and other factors effecting population fluctuations should be an ongoing component of TBNG research.

6) Monitoring should occur at a hierarchy of geographic scales.

TBNG- Begin to seek information on corridors, buffer zones as well as on additional area that effects the TBNG.

7) Inventory and monitoring efforts should include entire guilds or communities in cases where such sampling is sufficient.

TBNG- As gap analysis maps are produced, the monitoring of community and species representation at TBNG should measure growth in diversity and biomass over the years as grazing and mining activities are discontinued and the ecosystem regenerates.

8) The results of research projects and monitoring efforts should be closely integrated with management!

TBNG- The predominant consideration in TBNG management is presently livestock, livestock forage and game populations. Monitoring and studies has to shape the understanding of an entire ecosystem and all species. The "see-no-evil, hear-no-evil, speak-no-evil" policy in habitat management has to stop for this region to revive and survive.

Chapter 3

TBNG Management Reform

Federal Designations

There are limited options for a federal protective designation of TBNG. TBNG is a roaded, degraded ecosystem and does not have a 5,000 acre block of unroaded area and therefore does not qualify for a Federal Wilderness designation. Restoration and protection of this area requires creative legal and policy methods if it is to become federally protected. Possible existing designations include:

National Recreation Area (NRA)
National Park Act (16 USC § 460 et. seq.)

An area that can provide special management to its resources. The Glen Canyon NRA has cow-free zones, numerous hiking and boating access points and low-intensity management. The focus of an NRA is on recreation rather than resource extraction.

Research Natural Area (RNA)
National Forest Service Regulations (36 CFR § 251.23)

An area that is protected to preserve rare habitats and associated species. The RNA designation states "protect habitat for its own sake that is considered rare and unique." Since the prairie dog communities in TBNG are becoming increasingly rare and have a great many associated species, this may be an appropriate designation to seek. The Konza Prairie Preserve in southern Kansas is an example of a Research Natural Area.

National Monument
National Monument Act (16 USC § 1 et. seq)

With President Clinton considering the Arctic National Wildlife Refuge for National Monument status, this may not be far-fetched. A National Monument status could protect TBNG without going through Congress. This designation could prevent all grazing, mining and roading; restore the region; and encourage tourism.

National Park
National Park Act, (16 USC § 1 et. seq.)

A National Park designation would be the most favorable as it would provide TBNG with the most protection, allowing relief to an injured ecosystem. Also a National Park is education and resource oriented and could expose the public to the High Plains ecosystem. Local economies could benefit from a Plains Park with bison, native grasses, interpretive centers, and opportunities for recreation.

Legal Strategies

Legal action may be the best way to produce concrete management shifts during the short term, although in the long term a federal designation beyond "National Grassland" is preferable. USFS and BLM grazing allotments are being legally challenged all over the west on the grounds that grazing imposes a threat to riparian areas and sensitive or critical habitat, threatened and endangered species and water quality. Legal strategy may work well to fight the site specific issues of TBNG current management.

TBNG's ecological integrity has been put on the back burner by the Douglas County Ranger District and current grazing policies show a lack compliance with federal grazing laws and rules. Many allotments have no Allotment Management Plans. Most allotments have no routine monitoring program. There are even some allotments that have never been inventoried or cataloged for grass species or wildlife. The USFS is not doing their job by not monitoring the lands at TBNG. Prairie species stand defenseless due to biased alliances between livestock and federal management .[20]

In order to legalize protection for the prairie, appeals or a suit might be in order. USFS management in TBNG may be out of compliance with the following laws:

* *Taylor Grazing Act of 1934* (43 U.S.C. § 315-O-1; TGA) states that the governing federal agencies must " stop injury to public grazing lands by preventing overgrazing and soil deterioration." This act was developed following the decimation of "commons" rangeland in the early 1900's. *TGA* sets up an allotment and lease system, "to preserve the land and its resources from destruction or unnecessary injury." (43 U.S.C. 315a)

TBNG- Thunder Basin allotments have no routine monitoring program (see p. 23), and therefore the condition of the range in many areas is undetermined.

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[20] **Excerpt from 1991 letter from Douglas County Distric Ranger to Grazing Association Members in the TBNG regarding increased criticism of grazing on public lands-- "These are a few things that need to be done to ensure livestock grazing has a long future on public lands. Help us help you. If either of us are fail [to pass public scrutiny] , both of us lose."**

* *Multiple Use and Sustained Yield Act of 1960* (16 U.S.C.A. §§ 528 to 531; MUSYA) states that agencies managing public lands need to manage for multiple use. *MUSYA* defines multiple use as "the management of various sustainable resources of the national forests so that they are utilized in the combination that will best meet the needs of the American people making the most judicious use of the land...without permanent impairment of the productivity of the land, with consideration being given to the relative values of various resources, and not necessarily the combination of uses that will give the greatest dollar return or the greatest unit output." (MUSYA 15 CFR 531 (a).

If the best use of a piece of public land does not include grazing, *MUSYA* requires that the agency adopt a **no grazing policy**. (see *Sinapu v. Jerry Schmidt,* Sept. 2, 1994, pg 59; see Appendix C)

TBNG-- In TBNG grazing in riparian areas, hillsides, near uranium mines, near historic landmarks and in sensitive habitat may not be the best use of the land.

MUSYA* also demands that action "significantly affecting the quality of the human environment" needs to be researched through the preparation of an Environmental Impact Statement (EIS). EIS documentation and analysis notifies the public and Congress to the negative environmental impacts, alternatives of the action, cumulative effects and irreversible effects (43 U.S.C.A. § 4332). Major actions on public lands include **grazing programs (DEQ, Environmental Quality 182).

Administrative Law Judge John Rampton decided in *National Wildlife Federation v. BLM (UT-06-91-1994)* that an EIS for an entire resource area (in this case, the San Juan Resource area) may be insufficient to address every allotment within that area. An EIS for an individual grazing allotment with site specific considerations (e.g., riparian areas) was required for Comb Wash due to the degradation wrought by livestock grazing and the sensitive nature of the canyons (UT-06-91-01 Department of the Interior, Office of Interior and Appeals Div, Dec. 20, 1993)

TBNG- If "substantial questions have been raised whether a project may have significant effect upon the human environment, an EIS must be prepared" (*Sierra Club v., USFS, 843 F.2d 1190, 1193 (9th Cir. 1988)*). No grazing related EIS has ever been prepared for an allotment in TBNG. This creates an opportunity to find an area in TBNG used by hunters or fisherman that has been degraded by livestock-- "significant effect on the human environment."

**Endangered Species Act of 1973* (16 U.S.C.A. 1531 to1544; ESA) mandates that "each federal agency shall, in consultation with and with the assistance of the Secretary, insure that any action authorized, funded or carried out by such agency is not likely to jeopardize the continued existence of any endangered plant and wildlife species listed as endangered or threatened species or result in the destruction or adverse modification of habitat of such species as listed by the Secretary" 16 § 1536, 7(a)(1).

Pacific Rivers Council v. Thomas, 30 F.3d 1050 (9th Cir. 1994) found that the USFS grazing program was subject to the "may affect" standards of the ESA in cattle's adverse effects on endangered salmon species.

ESA also states that endangered species must be **managed with the objective of becoming delisted.** It is up to the agency to see how grazing effects endangered populations. Federal grazing practices may be inconsistent with ESA delisting objectives on an allotment with populations of endangered species.

TBNG- TBNG may be a reintroduction site for the black-footed ferret (USFS, 1990). Since black tailed prairie dogs are the primary food source to the black-footed ferret, it may violate ESA to manage with a Prairie Dog Management program, currently in place to poison prairie dogs on grazing allotments.

* *Federal Land Policy and Management Act of 1976* (43 U.S.C. §§ 1701-1784; FLPMA) states that "public lands be managed in a manner that will protect the quality of scientific, scenic, historical, ecological, environmental, air and atmospheric, water resource, and archeological value; that is, where appropriate, will preserve and protect certain public lands in their natural condition; that will provide food and habitat for fish and wildlife and domestic animals; and that will provide for outdoor recreation and human occupancy and use."

FLPMA also states that "permits can be revoked or suspended if the permittee violates or does not comply with Federal laws or regulations or State laws relating to the protection of air, water, soil and vegetation, fish and wildlife and other environmental values when exercising the grazing use authorized by the grazing permit." (36 CFR § 231.6 1977)

FLPMA provides guidelines for development and management of **Allotment Management Plans (AMP)**, the document that accompanies each federal grazing allotment. AMP's outline site specific information such as Animal Unit Months (AUM) , range improvements, wildlife habitat and permittee information. The AMP is a "**document prepared in consultation with the lessors or permittees involved, which applies to livestock operations on Forest Service or Bureau of Land Management lands, and which (*inter alia)* prescribes the manner in, and extent to which livestock operations will be conducted to include multiple-use, sustained yield, economic and other objectives as determined for the lands by the (*agency*)**" (43 U.S.C.A. § 1702 (k)). AMPs define range improvements that managing agencies plan to administer during the 10 year life of the plan; improvements that must prove consistent with the provisions of *FLPMA* 43 U.S.C.§1702 (k) as well as with the existing land management plan. In the case of grazing allotments that are inconsistent with a governing land plan, an AMP must include an expected date to come into compliance.

Permits on allotments are issued yearly explaining the type of livestock to be grazed on the allotment , the AUM and rotation schedules, seasonal pasture use and closures (43 C.R.F § 4130.6-1(a)). If the conditions of an annual permit is violated, the permit agreement can be canceled (43 C.R.F. § 4130.6-1(b)). AMP development or AMP changes are subject to NEPA and can be appealed under *FLPMA* (36 C.F.R.§ 251 or 36 C.F.R. § 217).

Under FLPMA, USFS and the BLM must determine if the practice of livestock grazing on an allotment is "a reasoned and informed decision as to whether grazing is in the public interest." (see *Sinapu v. USFS*, Appendix C)

TBNG-- There are over 100 allotments in TBNG that have never had an AMP completed. It could be possible to get an injuction on grazing until the AMPs are completed. (This could take a long time). As yet, the National Wildlife Federation (see *NWF v. USFS,* Appendix C) threatened get an injunction , but backed down due to local pressure from ranchers.

**National Forest Management Act of 1976* (16 U.S.C. § 200; NFMA) states that grazing permits issued must be consistent with the goals of corresponding land plans.

NFMA requires "Resource plans and permits, contracts, and other instruments for the use and the occupancy of National Forest system lands shall be consistent with the land management plans. Those resource plans and permits, contracts, and other such instruments currently in existence shall be revised as soon as practical to be made consistent with such plans." (16 U.S.C. §1604 (i)).

In implementing land plan regulations in AMPs, the Forest Service must include "a tabular display showing, in priority order, AMP revision, territory plans, and other grazing/browsing documents, and conform them to the management direction of the Forest Plan" (FSM 2200-Range Management, FSM 2213.1-Revision Schedules). In implementing a range analysis schedule, priority needs to be given to lands with riparian, soil, vegetation and water damage (FSM 2213.1 (1)).

TBNG- TBNG is so under supervised and researched, that range analysis has no routine or schedule. Transect monitoring is arbitrary and "ocular examines" are generally used for range assessment. This type of examination is arguably unscientific. Range damage is undetermined and unassessed and TBNG is clearly in violation of NFMA. Perhaps a grazing injunction is possible until a monitoring system is established. It could be that a court would freeze AUM levels until reliable monitoring occured.

Other Strategies

Legal routes may be costly, timely, and subject to congressional changes in the law. It is a strategy also often viewed as combative by community residents and allotment lessors. Whether legal victories bring grazing reform by the reduction of AUM's or complete livestock abolition, a community with a tradition in ranching will need assistance in acclimating to a new economy.

To accompany law suits, community outreach, town meetings, and bison ranching feasibility discussions may assist in easing High Plains residents toward an ecological reserve. In light of the controversies involved with livestock abolition on public land, attempts at community outreach may be better handled by groups not directly involved with legal action.

Chapter 4

Piecing Together an Ecosystem

Enforcing the Principles of Conservation Biology

What now remains compared with what existed then is like the skeleton of a sick man, all the fat and soft earth having wasted away, only the bare frame of the land being left.

(Erlich and Erlich, 1982)

Jumbled ownership patterns and intermittent distribution of wildlife populations leave TBNG fragmented in its present state. Currently TBNG can't support large bison herds or minimum viable populations of all native grasslands species (Forrest, 1994). However, there are opportunities for creating contiguous blocks with the goal of restoring this fractured ecosystem. A block of federal land in the Spring Creek Grazing Association, the center of TBNG, may be an area suitable for a reserve. This may be done through a land swap of BLM/USFS land for a small amount of private land.[21]

Within core habitat, management must allow nature to re-establish itself. Natural processes include nutrient cycling and flow of energy, disturbance regimes and recovery processes (succession), droughts and heavy rains, weathering and erosion, decomposition, herbivory, migration, predation, pollination, seed dispersal, parasitism, disease, mutation, gene

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[21] TBNG has a land swap program that attempts to consolidate federal land, however the program does not seek to consolidate federal lands that are ecologically sensitive or strategic in the purpose of creating core habitat.

Thunder Basin National Grasslands Proposed Core Reserve

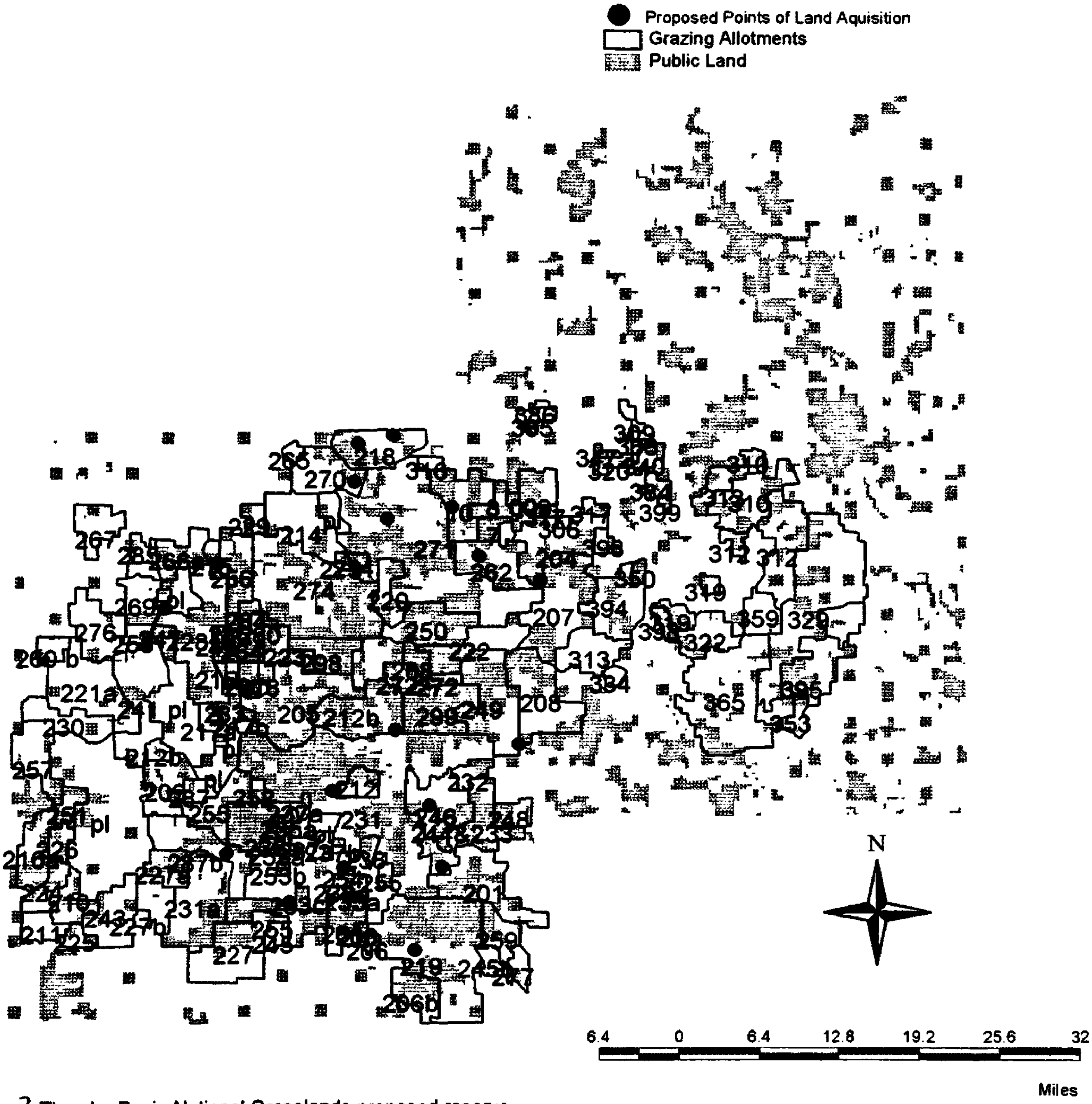

Figure 2.Thunder Basin National Grasslands proposed reserve, overlaid with grazing allotments with corresponding USFS allotment numbers.

flow, must also be restored and allowed to continue if the prairie ecosystem is to survive.

The following allotments fit together to form a core area of contiguous federal lands (see Figure 2; **Proposed Core Ecological Reserve**, pg. 36)

Allotments identified Core Habitat
(Douglas Ranger District)

206 B, Downs Allotment
vitals - This allotment has a total of 7643 acres, 3646 acres are USFS; 1044 AUM's in cattle. There are no riparian acres.
management aspects - The Allotment Management Plan (AMP) was done in 1987.

246, Rohleutner Allotment
vitals - This allotment has a total of 13196 acres, 5620 acres are USFS; 1723 AUM's in sheep and cattle. There are 10 riparian acres.
management aspects - The AMP was done in 1982 and is currently out of date: a violation of FLPMA and NFMA. Riparian analysis is needed and an EIS may be required.

201, Alexander -Allotment
vitals - This allotment has a total of 15999 acres, 5237 acres are USFS; 617 AUM's in sheep and cattle. There are no riparian acres.
management aspects - The AMP was done in 1981 and is currently out of date: a violation of FLPMA and NFMA.

010- Kara Community Allotment
vitals - This allotment has a total of 10830 acres, 6796 acres are USFS; 1710 AUM's in cattle. There are 551 riparian acres.
management aspects - The AMP was done in 1985 and is due for renewal in 1995. Riparian analysis is needed and an EIS may be required.

254, Wild Bill-Allotment
vitals - This allotment has a total of 800 acres, 160 acres are USFS; 28 AUM's in cattle. There are no riparian acres.
management aspects - The AMP was done in 1991.

287 Calamity Gulch Allotment
vitals - This allotment has a total of 17202 acres, 3369 acres are USFS; 567 AUM's in sheep and cattle. There are no riparian acres.
management aspects - There is no AMP; a violation of NFMA and FLPMA.

270 Ostlund Allotment-
vitals - This allotment has a total of 15318 acres, 2430 acres are USFS; 576 AUM's in cattle. There are 62 riparian acres.
management aspects - The AMP was done in 1984 and is currently out of date: a violation of FLPMA. Riparian analysis is needed and an EIS may be required.

266, Edwards Allotment
vitals - This allotment has a total of 6787 acres, 4440 acres are USFS; 1044 AUM's in sheep and horses. There are no riparian acres.
management aspects - The AMP was done in 1984 and is currently out of date: a violation of FLPMA.

269, Underwood Allotment,
vitals- This allotment has a total of 4418 acres, 1063 acres are USFS; 444 AUM's in sheep. There are no riparian acres.
management aspects- There is no AMP; a violation of NFMA and FLPMA.

258, , Taylor Allotment
vitals- This allotment has a total of 2511 acres, 1180 are USFS ; 273 AUM's of sheep. There are no riparian acres.
management aspects - The AMP was done in 1981 and is currently out of date; a violation of FLPMA and NFMA.

247, Sadler Allotment
vitals -There are a total of 3259 acres, 1760 are USFS; 461 AUM's of cattle and horses. There are no riparian acres.
management aspects - The AMP was completed in 1981 and is currently out of date: a violation of FLPMA and NFMA.

228, Mattheson Allotment
vitals - There are 19408 total acres, 4256 are USFS; 833 AUM's of sheep and horses. There are 21 riparian acres within the allotment
management aspects - There is no AMP; a violation of NFMA and FLPMA. Riparian analysis is needed and an EIS may be required.

275, Upper Basin Allotment
vitals - There are 2708 total acres, 775 are USFS; 177 AUM's of sheep. There are no riparian acres.
management aspects - The AMP was done in 1989.

215, Blow Out Allotment
vitals- There are a total of 985 acres, 640 are USFS; 191 AUM's of cattle. There are no riparian acres .
management aspects - The AMP was done in 1993.

217, Kane Allotment
vitals- There are a total of 4725 acres, 2098 are USFS; 456 AUM's of sheep. There are 51 riparian acres.
management aspects - There is no AMP; a violation of NFMA and FLPMA. Riparian analysis is needed and an EIS may be required.

212, Irwin Allotment
vitals- There are a total of 18287 acres, 11512 are USFS; 2683 AUM's of cattle. There are no riparian acres.
management aspects- There is no AMP; a violation of NFMA and FLPMA.

223, Mackey Allotment
vitals- There are a total of 5760 acres, 4550 are USFS; 149 AUM's of cattle. There are no riparian acres.
management aspects - There is a 1983 AMP that is no longer current; a violation of NFMA and FLPMA.

220, Small Allotment
vitals- There are a total of 6081 acres, 3065 are USFS; 605 AUM's of cattle. There are no riparian acres.
management aspects - There is an 1986 AMP which is up for renewal in 1996.

219, Ketelson Allotment
vitals- There are a total of 42019 acres, 19898 are USFS; 4560 AUM's of cattle. There are 245 riparian acres.
management aspects - There is a 1987 AMP. Riparian analysis is needed and an EIS may be required.

222, Lynch Allotment
vitals- There are a total of 18682 acres, 5135 are USFS; 1642 AUM's of cattle and horses. There are no riparian acres.
management aspects- There is a 1989 AMP.

264, Wilkinson Allotment
vitals- There are a total of 4043 acres, 2448 are USFS; 517 AUM's of cattle and sheep. There are no riparian acres.
management aspects- There is no AMP; a violation of NFMA and FLPMA.

286, Briggs Draw Allotment
vitals- There are a total of 1826 acres, 623 are USFS; 84 AUM's of cattle. There are no riparian acres.
management aspects- There is a no AMP; a violation of NFMA and FLPMA.

282, North Turner Allotment
vitals- There are a total of 1105 acres, 1105 are USFS; 172 AUM's of cattle. There are 31 riparian acres.
management aspects- There is no AMP; a violation of NFMA and FLPMA. Riparian analysis is needed and may need EIS.

274, Little Thunder Allotment
vitals- There are a total of 9327 acres, 5074 are USFS; 1480 AUM's of sheep. There are 65 riparian acres.
management aspects- There is a 1985 AMP which is out of date; a violation of FLPMA and NFMA. Riparian analysis is needed and may need an EIS.

288, Red Springs Allotment
vitals- There are a total of 7517 acres, 1845 are USFS; 176 AUM's of cattle and sheep. There are no riparian acres.
management aspects- There is a no AMP; a violation of FLPMA and NFMA.

255, Stoddard Allotment
vitals- There are a total of 17666 acres, 9990 are USFS; 2695 AUM's of sheep and horses. There are no riparian acres.
management aspects- There is an 1983 Allotment Management Plan (AMP), currently out of date; a violation of FLPMA and NFMA.

253, Steinle Allotment
vitals- There are a total of 2800 acres, 1600 are USFS; 415 AUM's of cattle . There are 25 riparian acres.
management aspects- There is a no AMP; a violation of FLPMA and NFMA. Riparian analysis is needed and may need an EIS.

259, Thomson Allotment
vitals- There are a total of 6600 acres, 3316 are USFS; 632 AUM's of cattle. There are no riparian acres.
management aspects- There is an 1981 AMP that stands five years out of date; a violation of FLPMA and NFMA.

249, Frog Creek Allotment
vitals- There are a total of 15573 acres, 9005 are USFS; 2590 AUM's of cattle and horses. There are 342 riparian acres.
management aspects- There is an 1985 AMP out of date at the end of 1995. The riparian acreage may require an an EIS.

283, Isenberger Allotment
vitals- There are a total of 2367 acres, 1089 are USFS; 270 AUM's of sheep. There are no riparian acres.
management aspects- There is an no AMP; a violation of FLPMA and NFMA.

262, Gordon allotment
vitals- There are a total of 8611 acres, 5454 are USFS; 2000 AUM's of cattle. There are 117 riparian acres.
management aspects- There is no AMP; a violation of FLPMA and NFMA. Riparian analysis is needed and may need an EIS.

268, North Rochelle Hills Allotment
vitals- There are a total of 3030 acres, 3030 are USFS; 374 AUM's of cattle. There are no riparian acres.
management aspects- There is a 1987 AMP.

235, Pellatz Allotment
vitals- There are a total of 1680 acres, 1200 are USFS; 327 AUM's of cattle. There are 103 riparian acres.
management aspects- There is an 1976 AMP, twenty years out of date; a violation of FLPMA and NFMA. Riparian analysis is needed and may need an EIS.

240, School Creek Allotment
vitals- There are a total of 21779 acres, 14780 are USFS; 632 AUM's of cattle. There are 213 riparian acres.
management aspects- There is an 1985 AMP, now out of date; a violation of FLPMA and NFMA. Riparian analysis is needed and may need an EIS.

231, Fiddleback Allotment
vitals- There are a total of 84102 acres, 41208 are USFS; 7788 AUM's of cattle and sheep. There are 249 riparian acres.
management aspects- There is no AMP; a violation of FLPMA and NFMA. Riparian analysis is needed and may need an EIS.

237, Betty Don Allotment
vitals- There are a total of 3071 acres, 1240 are USFS; 310 AUM's of cattle and sheep. There are 37 riparian acres.
management aspects- There is an no AMP; a violation of FLPMA and NFMA. Riparian analysis is needed and may need an EIS.

232, Dull Center Allotment
vitals- There are a total of 1947 acres, 1320 are USFS; 219 AUM's of cattle and sheep. There are no riparian acres.
management aspects- There is an 1983 AMP which is out of date; a violation of FLPMA and NFMA.

244, Tena Creek Allotment
vitals- There are a total of 7624 acres, 2620 are USFS; 767 AUM's of cattle . There are no riparian acres.
management aspects- There is an no AMP; a violation of FLPMA and NFMA.

299, Rosencrantz Allotment
vitals- There are a total of 12305 acres, 12305 are USFS; 2873 AUM's of cattle.There are 395 riparian acres.
management aspects- There is an 1986 AMP, which is out of date next year. Riparian analysis is needed and may need an EIS.

261, Weiss Allotment
vitals- There are a total of 3839 acres, 2360 are USFS; 1416 AUM's of cattle and sheep. There are no riparian acres.
management aspects- There is an 1987 AMP.

238, Reed Allotment
Vitals There are a total of 3154 acres, 2160 are USFS-; 514 AUM's of cattle and sheep. There are no riparian acres.
management aspects- There is an 1985 AMP, which is out of date; a violation of FLPMA and NFMA.

In order to link these allotments, a few chunks of private lands must be acquired through the Douglas Ranger District land swap program. These 15 pieces of private lands identified are strategic links connecting two big blocks of federal. (Pieces with prairie dog towns were opted for over inhabited areas.)

219, Kettleson Allotment-- The private pieces west of the Old Kettleson Place owned by Iberlin Ranch

201, Alexander - The private piece between Tena Creek and Cow Creek above Windy draw owned by Tillard "55" Limited

246, Rothleutner -The private piece between Meadow Creek and east fork southwest of Rothleutner Ranch

Area Between 238 , Reed and 254 ,Wild Bill - The private piece between Bruce Draw and Tin Can Creek

212, Irwin- The private piece between Beckwith Creek and Wildcat creek owned by Irwin Livestock Company

271 Keeline Allotment-- The private piece on Pipeline 4441 directly west of Wellman Ranch and a piece south of Thunder Creek by the corral; owned by Keeline Ranch Company

262 Gordon Allotment-- The piece of private land east of Lynch Roach and west of Fields draw and the piece between Thunder Creek and Prairie Creek owned by Billie Gordon

010- Kara Community Allotment -- Private piece of land below Cow Camp owned by East Cellers community

270 Ostlund Allotment---Private piece directly west Little RW Creek; ownership unlisted

275 Upper Basin Allotment---Private piece east of the Little Thunder Reservoir; ownership unlisted

228 Mattheson Allotment-- Private piece south of the Birdie Bit Ranch owned by Butch Mattheson

231 Fiddleback and 287 Calamity Gulch Allotments- Private piece on Dry Fork Creek southwest of Dilts Ranch owned by Two Rivers Ranch Inc. and Cannon Land and Livestock.

As these lands are prioritized and acquired, a piece of habitat can be established that is 213, 690 acres of existing federal land plus acreage added after acquisition of private land links. This additional acreage will depend on budget and availibility of federal pieces for trade in outlying isolated areas of the Powder River Basin. State lands, BLM lands and additional private inholdings interspersed in this reserve (see map) can either be swapped with agencies or private owners in exchange for isolated federal blocks on the periphery of TBNG. There is also a possibly for an inter-agency pact between Wyoming, BLM and USFS to manage a "new" TBNG with joint management goals. Eventually, a interim multi-agency pact would allow for incorporation of additional pieces of BLM[22] lands that border Thunder Basin to the east, to create a larger reserve. As the habitat base is established, federal protection in the form of national park, natural resource area, national recreation area, or national monument designation can be sought.

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[22] BLM land connects with TBNG on the Converse County / Niobrara County Line on the Tenth Standard Parellel

Conclusion

Transition to a Reserve

Whether TBNG can earn legislative protection, or whether protection comes slowly through suits and some lesser federal protection status, the transition should include the following modifications :

1) **Raise resources**. Whatever approach is taken towards developing a reserve, costs will certainly be incurred. Legal and lobbying expenses, community outreach costs, and the expense of restoration and re-introduction will require grants, fundraing and diverted federal subsidizes.

2) **Re-group**. The USFS has to work on a centralized form of management and move to mutually govern lands with the BLM and the State of Wyoming. Since TBNG is a jumble of land ownership, USFS management needs to be cooperative within these agencies.

3) **Re-prioritize**. Livestock should be phased out as public land continuity is established and private inholdings are aquired, with the possibility of compensating ranchers by re-directing grazing subsidies to individual permit holders.[23] Due to the ecological importance of a large grazing herbivore presence in TBNG, bison re-introduction should interpose a livestock phase-out. This process may take a while as bison are expensive and difficult to manage, but as the proper infrastructure is established, phase-out should begin immediately.

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[23] Federal subsidies cover "range improvements", fencing, stock pond development, weed erradication, and road building. This does not include predator or prairie dog control costs.

4) **Reform**. Management of TBNG should not be focused on resources, but on prairie species conservation and intense re-introduction and restoration. Missing species need to have suitable habitat and then be re-introduced.

5) **Re-populate**. Black tailed prairie dogs population numbers should stand around 10-30 prairie dogs per hecacre (O'Mielia, 1980). As species population re-establish, black-footed ferrets need to be re-established to one mother/pup pair per 30-50 hectarces, with one male overlapping the territories of several females (Harris, et al, 1989). In order to establish a minimum viable population numbers, 120-150 ferrets must exist in a population, connected to other populations throughout TBNG.

Mountain lion, coyote, black bear and studies in TBNG need to establish existing population numbers in order to see if minimum viable populations are already meet. [24]

Although bison management is costly and difficult to maintain, bison re-introduction is essential to an intact prairie ecosystem and favorable to cattle (see Appendix B). Re-introduction may move slowly to replace a cattle phase-out. The bison population should be between 125-193/100 hectacres according to the figures in Badlands (Berger, 1994) and Theodore National Roosevelt National Park (deJong, 1990), similar habitat types to TBNG.

6) **Revegetate.** Vegetation prototypes for healthy northern grasslands (not based on cattle forage prototypes) should be restored on bare overgrazed lands and in patches of crested wheat grass (exotic). A great deal of vegetation shifts

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[24] There is a population of black bear in the Laramie Peak area. (USFS, 1990)

should occur as livestock grazing is discontinued and native grazers are restored. Riparian revegetation and steam bank reclamation must also be a priority.

7) **Road rip**. Roads can remain until all private inholdings are acquired within the reserve boundary, then only Highway 450, Makey Road and North Lance Creek Road should remain. Road closures, ripping out roads and revegetation should ensue.

8) **Recreation**. There is not one developed camp site on the TBNG. Camp sites along the Powder and Cheyenne River, by bluffs, or in other scenic areas in TBNG should be developed.

Many prehistoric Indian sites exist on TBNG including campsites, lithic scatters, stone circle sites and butchering sites. An interpretative center for Native American history, grassland ecosystems and species would provide insight into the prehistory of TBNG. Recreation facilities, parking lots and road easements should be low impact in design.

9) **Revenue.** Communities should receive help adapting to a tourism based economy in the form of county and State loans. The TBNG covers eight counties that would gleen income from bird and wildlife viewers as well as recreationalists. Hunters and fishermen can expect a better backcountry experience without cattle upsetting water quality, fish and game populations or regional aesthetics. An economic study needs to be completed as soon as possible, to assess the benefits and liabilities to livestock phase-out.

Tourism would benefit communities far more than the amount of revenue grazing fees contribute to plains counties (Popper, 1991).

10) **Research-** The grasslands have been out of balance for over a hundred years. No one alive today has *seen*, let alone understands, the inter-workings of a healthy shortgrass prairie. As restoration and monitoring are integrated into the framework of a TBNG stewardship program, mushroom studies, lichen studies, invertebrate studies and minimum viable population studies of all prairie species have to constantly be in progress. This region needs to work as an ecosystem. Until resource managers know how the grasslands work, an ecosystem balance is an impossibility.

Thunder Basin is only one recovery site in the High Plains in need of relief from mining and grazing. The principles discussed in this document may be helpful in considering protection strategies ultimately used as the building blocks for protective legislation, the High Plains Ecosystem Protection Act. To restore the High Plains to its original functional state, the High Plains Ecosystem Protection Act needs to target the public lands throughout this region: the Niobrara River region in southwest Nebraska; Platte River Country in southeast Wyoming; the BLM lands and the Charles M. Russell National Wildlife Refuge; the Little Missouri Grasslands in Nebraska; and the western wheatgrass prairies of western North Dakota surrounding Roosevelt National Park.

Of course, these are only a few public areas within the High Plains that need restoration; the lands and potential are massive. The High Plains evolved along with herds of thundering bison, acres of prairie dog towns and seas of native grasses. This ecological profusion has earned the plains the distinction of the "American Serengeti." This diversity and abundance is the historic state rather than current form of this ecosystem. Only immediate recovery can salvage the ecological integrity of the High Plains.

Appendix A

Animals Co-occuring with Black Tailed Prairie Dog Towns
(Carlton, 1994)

Mammals

Coyote
Striped skunk
Mink
Long-tailed weasel
Badger
Raccoon
Red Fox
Mule Deer
Pronghorn
Eastern mole
Desert cottontail
Deer mouse
Thirteen-lined ground squirrel
Pocket gopher
Least chipmunk
Grasshopper mouse
American Bison
Plains pocket gopher
White Tailed deer
Western Harvest Mouse
Domestic cattle
Bobcat
Ord's Kangaroo Rat
House mouse
Domestic sheep
Domestic horse
Hispid pocket mouse
Black-footed ferret
White-tailed jackrabbit
Richardson ground squirrel
Wyoming pocket mouse
Southern plains woodrat
Plains cottontail
Least chipmunk
Porcupine
Elk
Spotted ground squirrel
Black-tailed jack rabbit
Northern grasshopper mouse

Birds

Golden eagle
Ferruginous hawk
American Crow
Red-tailed hawk
Swainson's hawk
Marshhawk (Northern harrier)
Prairie falcon
American kestrel
Burrowing owl
Great horned owl
Sage grouse
Blue-winged teal
Mourning dove
Killdeer
Common nighthawk
Mountain plover
Horned lark
American avocet
American coot
American robin
American white pelican
American widgeon
Biard's sandpiper
Baird's sparrow
Bald eagle
Barn swallow
Black-billed magpie
Black crowned night heron
Boat tailed grackle
Brewers blackbird
Brown-headed cowbird
Buff-breated sandpiper
California gull
Canada goose

Chestnut-collared longspur
McCown's longspur
Vesper sparrow
Lark bunting
Western kingbird
Loggerhead shrike
Brown-headed cowbird
Savannah sparrow
Cliff swallow
Snow bunting
Grasshopper sparrow
Great Blue heron
Greater yellowlegs
Herring gull
House sparrow
Lapland longspur
Lark bunting
Lesser prairie chicken
Lesser scaulp
Long billed-curlew
Marbled godwit
McCown's longspur
Mountain bluebird
Northern bobwhite
Northern harrier
Northern oriole
N. rough-winged swallow
Prairie falco
Red-tailed hawk
Ring-billed gull
Rough-legged hawk
Ruddyduck
Savannah sparrow
Scaled quail
Sharp shinned hawk
Short-eared owl
Snow goose
Spaugue's pipit
Turkey vulture
Vesper sparrow
Western kingbird
Yellow-headed black bird
Willet
Common grackle
Wilson's phalarope
Curved-billed thrasher
Double-crested cormorant
Eared greve
Eastern kingbird
Eastern meadowlark
European starling
Gadwall
Gray partridge
Green-winged teal
Great horned owl
Horned lark
Ladder-backed woodpecker
Lark sparrow
Lesser golden plover
Loggerhead shrike
Lesser yellowlegs
Mallard
Misissippi kite
Merlin
Mourning dove
Northern flicker
Northern mocking bird
Northern pintail
Pied-billed grebe
Redhead
Red-winged blackbird
Rock Dove
Sage grouse
Sage thrasher
Say's pheobe
Scissor-tailed flycatcher
Sharp-tailed grouse
Snow bunting
Sora
Swainson's hawk
Upland sandpiper
Water pipit
Western meadow lark

Amphibians

Leopard frog
Tiger salamander
Western toad
Green toad
Woodhouse toad
Great plains narrow mouthed toad
Chorus frog
Plains spadefoot frog
Couch's spadefoot frog

Reptiles

Eastern short-horned lizard
Sagebrush lizard
Red-sided garter snake
Prairie rattlesnake
Yellow mud turtle
Gopher bullsnake
Chihauhua spotted whiptail
Little stripped whiptail
Ornate boxturtle
Lesser earless lizard
Western diamondback rattler
Racerunner
Common gater snake
Texas spotted whiptail

Appendix B

American Bison

(Knowles, 1994)

*It is estimated that prior to European settlement of the plains, bison numbers were anywhere between 30 and seventy million.

*Between 1870 and 1900, the number was reduced to less than 1,000; 65,000 bison exist on ranches, reservations and parks today

* Migration patterns, indicative of the American bison would open.large swathes of land for evolutionary succession. This process would involve the arrival of prairie dogs that were attracted to disturbed areas. This was due to the high visibility of grazed grasslands allowing prairie dogs to watch for predators. *Dogs would turn up 4 tons of earth in a square acre and allow increased water absorption of 700 gallons.* Prairie dogs clipped forbs and left areas seemingly bare however dramatically increased the nutritional content of the grasses along the dog towns. However in studies, cattle grazing on dog towns weigh the same as cattle grazing apart from prairie dog towns. (O'Mielia, 1988)

* Bison also created large holes in the earth called wallows. Wallows turned into ponds or provided upturned soils and manure that became fertile sod. Bison bones provided calcium for plains herbivore

* Plains Indians were mainly farmers prior to the introduction of the horse by Spanish settlers in the mid-1500's The horse didn't influence the Indian populations immediately, but by the 1700's, many northern plain tribes have adopted bison hunting on horse back and became completely dependent on bison meat and hide for tribe existence

* Tribes would follow herds and used fire both to corner bison and to attract bison to fresh, tender new grass that grew subsequent to fires

* With white settlement, Gen. Sherman ordered that all bison be shot, skinned and sold until they were completely gone in the effort to subdue the Indians.

*Bison extirpation was a political objective and was quite easy due to the fact that they made easy targets at 7 ft high; to large to hide; herding behavior allowed hunters to slaughter several at a time

*With the bison disappearing, cattle was introduced in its absence.

Differences between Cows and Bison
(Knowles and Knowles, 1994)

Ecological Characteristics	Bison	Cattle
Mobility	high	low
Home size range	large	small
Grazing strategy	aggressive	passive
Water stress tolerance	high	low
Readily grazes steep slopes	yes/agile	no/clumsy
Requires water	24-96 hr intervals	12 hr intervals
Activity centered on	forage	water
Forage selection	generalist	specialist
Digestion efficiency	high	moderate
Wallows	yes	no
Cold Tolerance	high	low
Forage though snow	yes	no
Require supplemental winter feed	no	yes
Requires help calving	no	yes
Anti-predator behavior	strong	weak
Herding behavior	excellent	good
Longevity	20-30 years	10-15 years
Meat quality	excellent	good

Other Adaptations of Bison

-Bison are ice age animals; ice and snow is not a deterrent in foraging; can forage in snow, massive shoulders and hooves can forage in winter

-Bison are fast and agile and can deal with predators and fires

-Bison are migratory and follow the greening up after storms; do not just camp out like cows (Indians would travel 5-15 miles a day to keep up with the herds)

-Bison can go for 24 hours without water--do not hung out on riparian areas or need stock ponds

-Bison are more agile on treacherous topography

-Bison are general grazers and cattle are selective

-Bison digest prairie grass more efficiency

Bison are wild; cattle are domesticated

-Bison consume more graminoids than cattle--mitigated through historic migrations

-Bison need the prairie ecosystem incorporated with rearing and large pastures that may require multiple owner strategies (private, agency lands)

-Bison do not need predator control or stock pond development or crested wheat grass cultivation

-Bison ranching cannot be focused on maximum net production because as a wild animal bison have to be reared with an ecosystem in mind rather than a controlled operation with fenced pastures

-Bison are field Slaughtered vs. cattle in slaughter house

Appendix C

Grazing Challenge Overview

1)Gila Watch (GW)

Susan Schock; (505) 388-3449/2854; PO Box Silver City, NM

Although Gila Watch is currently involved with several livestock grazing cases, these are representative of GW strategy:

1) *Gila Watch v. US of America, Michael Espy, Jack Ward Thomas, Larry Henson, Regional Forest Supervisor, Carl Pence, Forest Supervisor of the Gila National Forest and Gerald A. Engel, Mimbres District Ranger* (No. Civil 94 1020 MV)

Claim-GW has brought this civil action under 5 USC § 701 et seq. asserting that the Forest Service has violated the *Wilderness Act* (16 USC § 1131, 36 CFR § 219.10 (e) and 36 CFR § 293.2 (1991) by allowing grazing in areas that were not grazed at the time of the establishment of the Wilderness Act.

> "The grazing of livestock shall be permitted where established prior to the date of this Act...." 16 USC § 1131 (d)(4)(2)

Request- That the USFS not grant permits for land not historically grazed prior to the Wilderness Act.

Status- No Decision as yet.

2) *Administrative Appeal on Allotments in Aldo Leopold Wilderness*

Claim- The Forest Service neglected to complete the EIS process on grazing allotments in Aldo Leopold Wilderness; the development of stock tanks in the Aldo Leopold Wilderness violates the Wilderness Act; grazing in riparian regions is an "unsuitable use of the land;" and livestock grazing in the Aldo

Leopold is economically unsuitable(*suitability* -16 U.S.C. § 1603 (g) (2) , 36 C.F.R. § 219.20 and 36 C.R.F. § 219.3).

Request- Assess the economic and ecological *suitability* of the area for livestock grazing and conduct NEPA process on Wilderness area allotments.

Status-No decision as yet.

Issue- USFS on issues of "*suitability*: the appropriateness of applying certain management practices to a particular area of land, as determined by an analysis of the economic and environmental consequences and the alternative uses forgone." (36 CFR 219.3)

2) Oregon Natural Desert Association (ONDA)

Bill Marlett, (503) 385-6908, 16 NW Kansas, Bend, Oregon 97701

ONDA, Rest the West, Oregon Nature Resources Council, Oregon Wildlife Federation, The Pacific Rivers Council, Portland Audubon, and National Trout Unlimited v. USFS

(attorney for ONDA- Michael Axline)

Claim- USFS issued a grazing permit, no. 01607, for the Camp Creek allotment within Malheur National Forest without first requiring the grazing permittee to obtain an Oregon water quality certificate. The action violates section 401(a) of the CWA, 33 U.S.C. § 1341(a).

Request- The USFS require the Cattle Creek Allotment permittee to obtain a state water quality permit before being granted permit renewal.

Status- Motion for summary judgement in April, 1995

Issue- Under Section 401 of the Clean Water Act, federal actions need to insure water standards if permits are issued on public lands. CWA states that an action needs a water quality permit in the case of an activity that "may" cause pollution to a navigable waterway. Evidence that cattle "may cause" pollution has been provided by grazing expert Denzel Ferguson. Jonathan Rhodes, a hydrologist for the Columbia River Inter-Tribal Fish Commission claims that cattle "affects water temperature, erosion, and sedimentation delivery due to its effects on riparian vegetation, soils, and channel morphology. "

The results of this case could be precedent setting and force all grazing permittees that "may pollute" using public lands to obtain state water quality certification . . It also may just become yet another level of bureaucracy.

3) Greater Gila Biodiversity Project (GGBP)

Kieran Suckling; (505) 538-0961; PO Box 742, Silver City, NM 88042

1) *Appeal of Toriette Allotment Management Plan*

Claim- The USFS has classified the renewal of the Toriette AMP a "minor management practice," and has labeled this allotment a "catagorical exclusion."This assertion is without just cause and sufficient scientific data.

The USFS is trying to issue grazing permits without doing an analysis of sensitive species threatening species such as the Apache Trout, Mexican Spotted Owl, and the Gila Trout and thus "fails to consult" under the provisions of ESA.

No cumulative effects analysis has been done on the condition of surrounding allotments as well as the streambank conditions, a process outlined by NEPA. No analysis has been done to determine the effects of "range improvements such as stock ponds and earthen dams.

Request- That the Toriette AMP categorical exclusion classification be reassessed and an injunction on grazing until an EA or EIS is completed on the allotment.

Status- No decision as yet.

Issue-USFS asserts that the revision of the Toriette AMP is an "implementation of a minor management practice to improve allotment condition or animal distribution," and therefore a categorical exclusion (EA documentation, FSH. 1909.15, Chapter 31,2, no. (31.2(9)).

GGBP claims that in making the Toriette Allotment a categorical exclusion, the USFS is violating NEPA, ESA, CWA and the Gila National Forest Management Plan. As yet, there is no ruling on the appeal.

2) *Michael v. District Ranger Steve Gunzel of Tonto National Forest; Supervisor Charles Bazan of the Tonto National Forest; Regional Forester Charles Cartwright and the US Forest Service*

Claim - The decision to re-instate grazing on the Pole Hollow Allotment has been made without consideration of: *suitability* of area for grazing (NFMA 16 U.S.C. § 1604 (g) (2)); reasonable alternatives (NEPA 42 U.S.C. § 4332 (2) (B)); that the decision is "arbitrary and capricious within the meaning of the Administrative Appeals Act" (APA, 5 U.S.C. § 706 (2).

Request- A judgment that the USFS is violating NEPA, NFMA and APA. An injunction on grazing the Pole Hollow Allotment or no more than 112 AUMs yearlong, until the NEPA and NFMA (*suitability* -16 U.S.C. § 1603 (g) (2) , 36 C.F.R. § 219.20 and 36 C.R.F. § 219.3) analysis is completed. No "range improvements" should be developed (fences, stock ponds, pipelines) until NEPA and NFMA are adhered to.

Status- No decsion as yet.

Issue- The Pole Hollow allotment was determined to be in poor condition in range analysis by the USFS and therefore deemed a high priority for legal challenge by the GGBP. In Hells Canyon, the Cayuse, Chalk Creek, Cold Springs, Cow Creek, Dobson Haas, Himmelwright, Mud Duck, Saddle Creek, Rhodes Creek, Schleur, Snell, Temp Sanke and Toomey allotments have been determined in poor condition.These allotments might be the first areas to address when challenging current grazing practices as they may be the most threatened.

4) National Wildlife Federation (NWF)

Tom France (406) 728-6705 240 North Higgins, Missoula, MT 59802

NWF v. USFS

Claim --Range management practices in the Beaverhead National Forest are out of compliance with NEPA (no site specific analysis of 136 of 166 allotments); only 125 allotments met monitoring standards outlined in the Beaverhead Forest Plan; AUMs within Beaverhead AMPs are too high; several riparian areas within the Beaverhead allotments have been classified by USFS to be in poor condition; resource damage from grazing is occurring due to non-compliance with NEPA and NFMA.

The plaintiffs also allege that the USFS is out of compliance with the Administrative Procedures Act (5 U.S.C. § 701 et seq. 1988, PA) that holds federal agencies responsible for action that is "arbitrary and capricious, an abuse of discretion, or otherwise not in accordance with the law" (5 U.C.S. § 706 (2) (A).

Request- An injunction on grazing permits until the Beaverhead allotments go through the EIS process and come up to code with their own Forest Plan.

Status- The NWF offered the USFS ten years to come into compliance with their own laws. The settlement is still being decided. The NWF asked that the USFS do NEPA on 10% of the allotments a year over the 10 year period.

Issue-This case could set a USFS position for revamping AMP development and renewal. A ten year process to update western USFS grazing management policies could take a grave ecological toll on over-grazed federal lands.

5) Joe Feller, University of Arizona Law School/ NWF

(303) 786-8001; 2260 Baseline Road ,#100; Boulder, CO 80309

National Wildlife Federation, Southern Utah Wilderness Alliance and Joe Feller v. Bureau of Land Management (UT-06-93-01)

Claim- *BLM* neglected to notify affected interests (Joe Feller) of a grazing permit renewal to the Ute Mountain Indian Tribe; the BLM neglected to allow affected interests opportunity for public comment on permit renewal; the BLM violated NEPA for not conducting a site specific EIS on five canyons within the Comb Wash allotment within the San Juan Resource Area; the BLM violated *FLPMA* for reissuing a permit without "reasoned and informed decisions of whether the canyon area was in the best public interest to have grazed"; the BLM violated the San Juan Resource Management Plan for setting excessive utilization limits in Comb Wash which was given a "poor" rating in BLM range monitoring.

The BLM disregarded the health and preservation of visual quality, riparian areas, vegetation, recreation use, erosion and wildlife habitat in its decision to graze five canyons within the Comb Wash allotment.

Request- Fence cattle out of sensitive riparian areas until the completion of the EIS on grazing impacts in the Comb Wash allotment.

Status- Case won in 1994; appealed in 1994.

Issue- The San Juan area-wide EIS for its Resource Management Plan did not necessarily apply to the site specific features of canyons and riparian areas within Comb Wash.

Expert witness Robert Ohmart of the Arizona State University gave testimony explaining that the San Juan Resource Area RPM/FEIS "is pathetically short on any understanding or appreciation of efforts to appropriately [sic] manage riparian habitats in the Comb Wash allotment. This document is so generic it could fit any place in northern Arizona or southern Utah if you change the names of the places to protect their identity. That document is meaningless as far as giving anyone any biological assessment of the riparian habitat or wildlife. I mean, there's only four kinds of wildlife in the document. If you aren't a sheep, if you aren't a deer, if you aren't an antelope or a peregrine falcon, you're not even wildlife." (Appeal to BLM of San Juan Resource Area RMP, pg. 9)

TBNG could be challenged for allotments with insufficient NEPA consideration if the area wide EIS for the Wallowa-Whitman Comprehensive Management Plan neglected to address site specific considerations within allotments. In the Feller case, site specific areas that Judge Rampton ruled canyons may need a special site specific NEPA process. Due to their delicate nature, cows were fenced out of two desert canyons in the Comb Wash Allotment.

6) Ochoco Resources and Recreation Association

Tonia Wolf; 281451 Miller Rd.; Prineville, OR 97754;(503) 317-9464

Appeal of Sunflower Grazing Allotment to Regional Forester, Ochoco, NF

Claim- EA on the Sunflower Allotment in the Ochoco National Forest in Eastern Oregon does not consider a "No Grazing" alternative (NEPA)

Request- Full consideration and analysis of a no grazing alternative

Status- Injunction on livestock grazing implemented in 1994; EA completed in 1995. ORRA did not appeal EA.

Issue- As allotments come up for renewal, an EIS or EA must include a no-grazing alternative.

7) Sinapu

Michael Robinson, PO Box 3243, Boulder CO 80307 (303) 494-7920

Administrative Appeal of North Hunt Allotment to Forest Supervisor of the Routt National Forest

Request- Sinapu requests an injunction on grazing on North Hunt until a detailed sustainability study and range analysis are completed.

Claim-The *Finding Of No Significant Impact* (FONSI) classification on North Hunt Allotment is inappropriate because: the allotment is overgrazed; no scientific data exists on wildlife within the allotment boundaries; USFS has failed to consult with the US Fish and Wildlife Service on environmental impacts to the peregrine falcon; the allotment is unsuitable to grazing because of impacts on wildlife, soil, riparian habitat. (According to wildlife biologist Kathleen Nelson, the streambank erosion on Spronks Creek, located within the North Hunt Allotment is "probably the worst in the district.")

(*When the USFS got wind of the Sinapu challenge of cows on North Hunt, the AMP switched cattle AUM stipulations to sheep. Sinapu challenged this switch as illegal under NEPA*).

Sinapu also requests an EIS for the North Hunt drainage complete with analysis on the "effects of livestock grazing on Spronks Creek, its headwaters, and associated riparian areas" (North Hunt Appeal, pg. 3). The EIS needs to include an analysis of land "*suitability*" by examining "the appropriateness of applying certain management practices to a particular area of land, as determined by an analysis of the economic and environmental consequences" (16USC(g)(2);36 CFR 219.20(a).

Status- Appeal was successful and all livestock have been removed from the 6,575 acre North Hunt Allotment.

Issue- The USFS allowed grazing without examining the "suitability" in the EA of North Hunt for livestock. "The first determination--the suitability of the lands for grazing--must be made before a decision to authorize grazing can be made, but a grazing suitability determination does not necessarily lead to a decision to graze those lands. Even though lands may be suitable for grazing, other resource objectives may take precedence over grazing livestock; for example, protection needs of wildlife habitat might take a higher priority in a given area, and thus grazing would be incompatible with this objective" (*Federal Register*, Vol. 59, No. 81, April 28, 1994).

8) National Wildlife Federation (NWF)/Nevada Wildlife Federation,

Peter Frost, National Wildlife Federation, 921 S.W. Morrison, Suite 512, Portland, OR 91184

(503) 222-1429

NWF, Elko County Conservation Association, Nevada Wildlife Federation v. US Forest Service, Jack Ward Thomas, Humboldt National Forest Supervisor R.M "Jim" Nelson

Claim- By allowing livestock grazing on allotments within the Humboldt National Forest, the USFS is in violation of NEPA, NFMA, as well as the Administrative Procedures Act.

Request- Ruling that the USFS is in violation of NFMA, NEPA, and APA. Injunction on grazing until USFS comes into compliance with NEPA and NFMA.

Status- Complaint filed in March, 1995.

Issue- This case is very similar to NWF case in the Beaverhead National Forest (page 12). The appellants, according to Dan Hines (American Wildlands, Reno, NV.) want the USFS to do EIS on Humboldt National Forest grazing allotments, update their AMP, and fence off some riparian areas. As with the Beaverhead case, appellants are willing to allow the USFS months/years to come into compliance.

Bibliography

Alverson, William S.; Kuhlmann, Walter; Waller, Donald M., 1994. Wild Forests: Conservation Biology and Public Policy. Island Press, Covelo, CA

Biodiversity Legal Founation. 1994. Petition to Classify a Black Tailed Prairie Dog as a Catagory 2 Candidate Species.
Office of Endangered Species; U.S. Fish and Wildlife. Washington D.C.

Brown, Lauren. 1989. The Audubon Society Nature Guides: Grasslands. Alfred Knopf Books, New York.

Berger, Joel E. and Carol Cunningham. 1994. Bison: Mating and Conservation in Small Populations. New York: Columbia University Press.

Bureau of Land Management, US Department of the Interior. 1991. State of Wyoming, Land Status Map, US Government Printing Office.

Bureau of Land Management, US Department of the Interior. 1979. State of Wyoming, Mineral Status Map.

Clark, TW. 1974. "Prairie Dogs: an historic view of some ecological and economical considerations." Madison, WI.

Clark, TW. 1977"Ecology and Ethnology for the white-tailed prairie dog Cynomys leucurus." Publ. biol. Geol. No. 3, Milwaukee Public Museum.

Clark, TW. 1979."The hard life of the prairie dog". National Geographic, 156(2): 270-281.

Clark, TW. 1989. Conseravtion Biology and the Black Footed Ferret. (Wildlife Preservation Trust International. Philidelphia, PA.

Clark, TW. 1974. "Prairie Dogs: an historic view of some ecological and economical considerations." Madison, WI.

Cody, Martin L. and Jared M. Diamond. 1975. "Ecology and Evolution of Communities." Cambridge: Harvard University Press.

Coggins, George; Wilkinson, Charles; John, Leshy. 1993. Federal Public Land and Resoures Law, The Foundation Press, Westbury, NY.

Dary, David. 1974. The Buffalo Book. Avon Books, New York.

Davis, Tony. 1994. "Struggle for the Last Grass," High Country News May 2, 1994; Vol. 26, No. 8

Feller, Joe; Rait, Ken; Strickland, Rose; Wald, Johanna. 1992. How Not to be Cowed. Natural Resources Defense Council & Southern Utah Wilderness Alliance, Salt Lake City, Utah, 1992

Ferguson, Denzel and Nancy. 1994. Sacred Cows at the Public Trough, Maverick Publications, Bend, Oregon.

Fleischner, Thomas L. 1994. "Ecological Costs of Livestock Grazing in Western North America," Conservation Biology, 10: 629-64.

Foreman, Dave. 1992. "Developing a Regional Wilderness Recovery Plan." Wild Earth Special Issue. Canton, NY: The Cenozoic Society.

Forrest, Steve. Telephone Interview. May 1994- Oct. 1995

Forrest, Steve and Roemer, Dave. 1994. "Prairie Dog Poisoning in the Northern Plains: An Analysis of Programs an Policies." Draft Document, unpublished.

Forrest, SC., Clark, TW, Richardson L., and Cambell, TM. 1985. "Black-footed Ferret Habitat: some managment and re-introduction considerations." Wyoming BLM Wildlife Bulletin. No. 2. Cheyenne, WY.

Frankel, O.H. and Michael E. Soulé. 1981. Conservation and Evolution. Cambridge: Cambridge University Press.

Franklin, I.R. eds. 1980. " Evolutionary change in small populations. " Conservation Biology: An evolutionary-ecological perspective. Sunderland, MA: Sinauer Assoc.

Grumbine, R. Edward Environmental Policy and Biodiversity. Island Press, Covelo, CA. 1994

Glustrom, Leslie. 1991. Participating in Livestock Grazing Decisions on the National Forests , Prescott, AZ.

Hansen, RM. and JK Gold, 1977. "Black-tailed prairie dogs, desert cottontails and cattle trophic relations on the shortgrass range". Range Management. Jan. 30:307-313

Jackson, Wes. 1993 "Ecological Determinism vs. the Jeffersonian Ideal," The Land Report. #48, Fall

Jacobs, Lynn. 1991. Waste of the West. Tuscon, Arizona.

Keopsel, Kirk. Interview. September 18, 1994.

Knowles, CJ, PR. Knowles. 1994. "A review of the black tailed prairie dog literature in relation to rangelands administered by the Custer National Forest" USDA, Forest Service.

Licht Daniel. 1994. "The Great Plains-Part 1." Wild Earth (Summer 1994, pgs 47-53).

Licht Daniel. 1994. "The Great Plains-Parts 2." Wild Earth (Fall 1994, pgs 31-36)

Matthews, Anne. 1992. Where the Buffalo Roam. Grove Press, New York.

Noss, Reed. 1992. "The Wildlands Project Conservation Strategy" Wild Earth: The Wildlands Project (Special Issue, pg 10-25)

Noss, RF and A. Cooperrider. 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Defenders of Wildlife and Island Press, Washington DC.

O'Mielia, ME. 1982. "Some consequences of competition between prairie dogs and beef cattle." Range Management. 35:580-585.

O'Mielia, ME. 1980. "Competition between prairie dogs and beef cattle for range forage. MS Thesis." Oklahoma State University. Stillwater, OK.

Randall, O'Toole. 1994. "Reforming the Western Range." Different Drummer (Volume 1 Number 2, Spring, pgs. 7-15)

Peterson, Roger Tory. 1990. Western Birds. Houghton Mifflin Company, New York.

Pitcher, Don. 1991. The Wyoming Handbook. Moon Publications, Chico, CA.

Shull, A.M. and A.R. Tipton. 1987. "Effective population size of bison on the Wichita Mountains Wildlife Refuge." Conservation Biology . 1:35-41.

Soule, Michael. 1992. "A Vision for the Meantime" Wild Earth: The Wildlands Projects:*Special Issue,* (pgs. 7-8).

Soulé, Michael E. 1987. Viable Populations for Conservation. Cambridge: Cambridge , University Press.

Soulé, Michael E. and Kathryn A. Kohm. 1989. Research Priorities for Conservation Biology. Washington, D.C., Island Press.

USDA and APHIS, 1993. "Animal Damage Control Plan for Public Land Administered by the United States Forest Service Administrative Unit." Medicine Bow National Forest.

USFS. 1985. "Resource Management Plan for the Medicine Bow National Forest and Thunder Basin National Grassland." US Dep't of Agriculture.

USFS. 1990. "The Douglas Ranger District: Medicine bow National Forest & Thunder Basin National Grasslands--Management Situation Narrative." US Government Printing Office.

USFS. 1963-1995. "Allotment Files on Inkara, Spring Creek and Thunder Basin Allotment Leases." Douglas Ranger District. WY.

USFS, 1989. "Management of the National Grasslands."
Symposium on the United States Dep't of Agriculture in Historical Perspective at the Iowa State University. Photocopied.

Wuerthner, George. 1995. "Last Chance for the Prairie Dog," Wild Earth, (Issue 12, Spring)

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ORIGINAL PAPER

High prevalence of *Yersinia pestis* in black-tailed prairie dog colonies during an apparent enzootic phase of sylvatic plague

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Abstract Sylvatic plague (*Yersinia pestis*) was introduced into North America over 100 years ago. The disease causes high mortality and extirpations in black-tailed prairie dogs (*Cynomys ludovicianus*), which is of conservation concern because prairie dogs provide habitat for the critically endangered black-footed ferret (*Mustela nigripes*). Our goal was to help elucidate the mechanism *Y. pestis* uses to persist in prairie ecosystems during enzootic and epizootic phases. We used a nested PCR protocol to assay for plague genomes in fleas collected from prairie dog burrows potentially exposed to plague in 1999 and 2000. No active plague epizootic was apparent in the 55 prairie dog colonies sampled in 2002 and 2003. However, 63% of the colonies contained plague-positive burrows in 2002, and 57% contained plague-positive burrows in 2003. Within plague-positive colonies, 23% of sampled burrows contained plague-positive fleas in 2002, and 26% contained plague-positive fleas in 2003. Of 15 intensively sampled colonies, there was no relationship between change in colony area and percentage of plague-positive burrows over the two years of the study. Some seasonality in plague prevalence was apparent because the highest percentages of plague-positive colonies were recorded in May and June. The surprisingly high prevalence of plague on study area colonies without any obvious epizootic suggested that the pathogen existed in an enzootic state in black-tailed prairie dogs. These findings have important implications for the management of prairie dogs and other species that are purported to be enzootic reservoir species.

Keywords *Cynomys ludovicianus* · Disease · Montana · Nested PCR · *Pla* gene

Introduction

Sylvatic plague is caused by the bacterium *Yersinia pestis*, which was introduced into North America from Asia about 100 years ago (Kartman 1970; Perry and Fetherston 1997; Gage and Kosoy 2005). Like other introduced diseases, plague poses a significant threat to native species, particularly those that are rare and endangered (McCallum and Dobson 1995; Thorne and Williams 1988; Woodroffe 1999; Daszak et al. 2000). Plague causes high mortality in black-tailed prairie dogs (*Cynomys ludovicianus*), and is a major factor in the range-wide decline of the species (Biggins and Kosoy 2001; Cully and Williams 2001). Fleas are the primary vectors of sylvatic plague and sociality of prairie dogs facilitates rapid spread of the disease between individuals and among colonies.

Plague has acted in concert with habitat conversion, poisoning, and recreational shooting over the last century to decrease the area occupied by black-tailed prairie dogs by 90–99%, which corresponds to a loss of approximately 40 million hectares of habitat (Anderson et al. 1986; Miller et al.1994; Van Putten and Miller

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1999; Forrest 2005). Status of the black-tailed prairie dog is of considerable conservation concern for biologists working to maintain biodiversity because the species creates habitat or is prey for several rare and declining species (Miller et al.1994; Kotliar et al. 1999; Miller et al. 2000). For example, the highly endangered black-footed ferret (*Mustela nigripes*) depends on black-tailed prairie dog colonies for its primary habitat, as do several non-endangered species, including mountain plovers (*Charadrius montanus*), burrowing owls (*Athene cunicularia*), and hawks (*Buteo* spp.) (Knowles et al. 1982; Thorne and Williams 1988; Seery and Matiatos 2000; Restani et al. 2001). Negative effects of plague on prairie dogs indirectly hamper conservation efforts of these species. Black-footed ferrets also suffer a direct effect of plague epizootics because they are highly susceptible to the disease (Williams et al. 1994).

Host species of sylvatic plague are classified as either epizootic (amplifying/susceptible) or enzootic (resistant/reservoir) (Lechleitner et al. 1968; Perry and Fetherston 1997; Gage and Kosoy 2005). In general, resistant hosts transmit the pathogen via fleas to susceptible hosts, thereby triggering an epizootic. It is during epizootic phases that declines in abundance of susceptible species like prairie dogs are observed. Colonies hundreds of hectares in size can be decimated by plague within only a few weeks (Lechleitner et al. 1968; Rayor 1985; Menkens and Anderson 1991; Cully and Williams 2001). In addition to the immediate demographic consequences, these population bottlenecks reduce long-term genetic diversity of prairie dog populations (Trudeau et al. 2004). During the enzootic or maintenance phase, however, there is no widespread mortality in susceptible species and spread of the disease appears highly restricted (Gage and Kosoy 2005).

Epizootic outbreaks of sylvatic plague are typically explained by the presence of resistant reservoir species, which maintain the disease in the environment and are the source of subsequent epizootics in susceptible hosts (Perry and Fetherston 1997; Cully and Williams 2001; Gage and Kosoy 2005). Plague can theoretically be retained in the environment without causing devastating epizootics in susceptible hosts (Keeling and Gilligan 2000; Davis et al. 2004), possibly by cycling within and between reservoir species that are not susceptible to the disease (Barnes 1982). Many common and widespread species are believed to be resistant to the disease, including most carnivores and some rodents (Lechleitner et al. 1968; Barnes 1982; Perry and Fetherston 1997; Biggins and Kosoy 2005). Diseases with purported reservoir hosts are not constrained by the density of their epizootic hosts, which extirpates these populations, yet allows the disease to persist in the environment in enzootic hosts (Barnes 1982). Mitigating plague's effects on the prairie dog ecosystem is proving difficult due its unpredictable and recurrent nature and the distribution and abundance of both susceptible and resistant hosts (Davis et al. 2004).

Montana contains large areas important for conservation of black-tailed prairie dogs and their habitat associates. Colonies occupy an estimated 36,000 hectares, most of which are located in the north-central part of the state (Faunawest Wildlife Consultants 1999). Here colonies are separated by short distances and vary widely in overall size and population density. Our study area, the Fort Belknap Indian Reservation (FBIR), resides within this region and contains about 200 prairie dog colonies as well as reintroduced black-footed ferrets, mountain plovers, and burrowing owls. Fleas from prairie dog burrows on two colonies tested positive for sylvatic plague in 1999, a discovery which coincided with disappearances or significant declines of colonies in 1999 and 2000. Of the 8 flea species common to FBIR, about 70% of the flea fauna is composed of *Oropsylla hirsuta* and *O. tuberculata cynomuris* (Young unpublished data), which feed exclusively on prairie dogs (Cully and Williams 2001). *Pulex irritans* has a wide host preference and constitutes about 15% of the flea assemblage (Young unpublished data).

Collecting and testing fleas for the presence of *Y. pestis* is a potential tool in the surveillance of sylvatic plague. *Y. pestis* accumulates in the foregut of infected fleas (Perry and Fetherston 1997), and PCR-based methods provide a useful and sensitive means to detect the pathogen (Englethaler et al. 1999). We used a very sensitive PCR procedure to detect the presence of *Y. pestis* genomes within fleas collected from black-tailed prairie dog burrows on FBIR in 2002 and 2003. Our goal was to help elucidate the mechanism *Y. pestis* uses to persist in the prairie ecosystem during enzootic and epizootic phases by testing fleas collected from prairie dog colonies that had potentially been exposed to plague in 1999 and 2000.

Methods

Sample collection and DNA extraction

Between May and August 2002 and 2003, we collected fleas from burrows of 55 black-tailed prairie dog colonies on FBIR. We collected fleas by pushing a white flannel cloth into active prairie dog burrows (Ubico et al. 1988). Burrows were determined to be active by the presence of fresh droppings and diggings. Fleas were removed from the cloth and stored in 3.6 ml cryotubes filled with 95% ethanol. We did not identify fleas to species and pooled all fleas sampled from a burrow on each sampling occasion for DNA extraction and plague assays. Sampled burrows were distributed throughout the extent of each colony, and we took a GPS location at each burrow. We sampled 36 colonies at least once during both years of study.

The perimeters of 15 colonies were mapped with GPS technology from 2001 to 2003 (Geoscience Associates 2003), and we extensively sampled these 15 colonies for fleas throughout 2002 and 2003: late May/early June, late June/early July, and late July/early August. We sought to associate any change in area of the prairie dog colony with seasonal prevalence of plague**.** Following convention, we used area of prairie dog colonies as an index to abundance (i.e., population size) (Miller et al. 1994; Van Putten and Miller 1999; Cully and Williams 2001; Forrest 2005). Study colonies were selected based on previous declines in size suggestive of past plague epizootics or their proximity to infected colonies.

We extracted DNA from whole fleas with the Easy DNA kit (Invitrogen Life Technologies, Carlsbad, CA). Manufacturer's protocols were followed in modified form for mouse tail extraction (protocol 8, Invitrogen Life Technologies) using 0.1 of the recommended volume. Fleas were washed in 0.15% saline solution, added to 1.5 ml micro-centrifuge tubes, and crushed with a closed 1000 µl pipette tip. A chloroform extraction followed as described by the manufacturer. Supernatant was washed with 100 µl of 100% ethanol (–20°C) and set on ice for 30 min. Centrifugation followed at maximum speed for 10min at 4°C. We decanted ethanol and dried the resulting pellet in a vacuum centrifuge. The pellet was resuspended in 30 µl of TE and stored at –70°C.

Bacterial strains and cultivation

We obtained *Y. pestis* strain A1122 var. *orientalis* from the Centers for Disease Control, Ft. Collins, CO. This strain lacks the 70-kb pCD1 virulence plasmid and is not pathogenic. *Y. pseudotuberculosis* (ATCC #29833) and *Y. enterocolitica* (ATCC #23715) were obtained from the American Type Culture Collection. Cultures were grown in Brain-Heart Infusion (BHI) broth with agitation at 37°C. We stored 1-ml aliquots from overnight broth cultures at –70°C. Counts were performed to determine total numbers of colony-forming units (CFU) in each stock culture. Total genomic DNA was extracted using Easy-DNA (Invitrogen Life Technologies) from ~1.3×10^7 CFU *Y. pestis*, 4×10^9 CFU *Y. pseudotuberculosis*, and 3.2×10^9 CFU *Y. enterocolitica*; CFU:bacteria ratio for *Y. pestis* is probably <1 due to the tendency of this organism to clump in broth medium. DNA was dissolved in 50 µl tris-EDTA (TE, 10 mM tris-HCL pH 8.5/1 mM EDTA).

Nested PCR

A nested PCR, based on an assay described by Hinnebusch and Schwan (1993), was designed to amplify a 110-bp fragment of the plasmid-encoded *pla* (plasminogen activator) gene unique to *Y. pestis* (Sodeinde et al. 1988). A nested PCR protocol was used because the desired sensitivity could not be achieved with a single primer set. All PCRs were carried out using either a MJ Research PTC 200 Thermocycler or an Eppendorf Mastercycler Personal Thermocycler. The initial step was carried out using primers ypl3 and ypl4 (5′–3′ catccggctcacgttattatggtacc, 5′–3′ ctgtaggaagctcaacatccaag) modified from primers yp1 and yp2 described by Hinnebusch and Schwan (1993), in a 50 µl reaction containing 1 Hotstart *Taq* Polymerase bead (Promega Taqbead 1.25 u/bead), 1× $MgCl_2$ free buffer, 0.2 mM dNTP, 1.5 mM $MgCl_2$, 1.0 µM primers. Settings were 1 cycle at 95°C for 5 min, 30 cycles at 95°C for 1 min, 50°C for 1 min, and 72°C for 2 min, 1 cycle at 72°C for 8 min. This initial PCR product was 460 bp in length. Nested PCR used primers ypl5 and ypl6 (5′–3′ cacacctaatgccaaagtct-ttgcgg, 5′–3′ gtggagattctgtctctattggcg). Nested PCR was carried out by using 5 µl of product from the initial PCR step in a 50 µl reaction containing the same concentration of reagents and subjected to the same conditions as the initial PCR step. Sensitivity and specificity of the assay were determined by amplifying 10-µl templates of 10-fold *Y. pestis* DNA dilutions and 10 µl 1:10 dilutions of *Y. enterocolitica* and *Y. pseudotuberculosis* DNA. PCR products were examined by electrophoresis on 1.5% or 2% TBE agarose gels stained with ethidium bromide. Gels were photographed with an electrophoresis documentation system (Kodak Electrophoresis Documentation and Analysis System 120). Amplification of the *pla* fragment from *Y. pestis* DNA extracted from fleas was carried out with 5 µl of undiluted template. DNA extracted from *Y. enterocolitica* and *Y. pseudotuberculosis* and sterile water (5 µl each) were used as negative controls, and DNA extracted from *Y. pestis* strain A1122 and diluted 10^{-6} (5 µl) was used as a positive control in all PCRs.

Later, one negative and several positive flea DNA samples and the above-described positive and negative controls were reamplified to provide an example of assay results (Fig. 1); for this purpose we used 1 µl of template and electrophoresed the resulting amplicons on a 2% agarose gel.

Results

Y. pestis DNA diluted 10^{-1} through 10^{-6} yielded 110-bp products. In a later experiment, similar results were obtained with 1 μl of the 10^{-6} dilution (Fig. 1), for an apparent sensitivity of ~0.3 CFU per sample (actual sensitivity is less than this because of bacterial clumping and the likely presence of multiple copies of the *pla*-encoding plasmid per *Y. pestis* genome). No products were amplified from *Y. enterocolitica* or *Y. pseudotuberculosis* at any concentration tested. These results confirm that the nested PCR used in this study is both specific and highly sensitive.

We sampled fleas from 55 colonies in 2002 and 2003, with 36 colonies sampled at least once both years (Table 1). Fig. 1 shows a sampling of *pla* amplicons from fleas collected in this study. Overall, 63% (n = 30 colonies) of colonies had at least one plague-positive flea sample in 2002, and 57% (n = 24 colonies) of colonies had at least one plague-positive flea sample in 2003. Plague-positive colonies were distributed throughout FBIR. For plague-positive colonies, 23% (mean ± SE, 3.9 ± 0.5 plague-positive burrows/colony) of sampled burrows had plague-positive fleas in 2002, and 26% (2.3 ± 0.3 plague-positive burrows/colony) had plague-positive burrows in 2003.

We collected fleas from 15 colonies over 3 time periods in 2002 and 2003 (Table 2). Although percentages of plague-positive colonies varied among the 3 sample periods, plague was most detectible between late May and early July (Fig. 2). These results were also consistent with the entire dataset: for all plague-positive burrows sampled in 2002, 72% were from late June/early July, and 72% of all plague-positive burrows sampled in 2003 were from late May/early June.

Of the 15 intensively sampled colonies, 4 colonies increased in area (ha) between 2001 and 2002, and between 2002 and 2003 (Table 3). Six colonies decreased in area between 2001 and 2002, and a different group of five colonies decreased in area between 2002 and 2003. No colony decreased in area both years. Of the 15 intensively sampled colonies, a regression of percentage change in colony area between 2001 and 2002 against percentage of plague-positive burrows in 2002 was nonsignificant ($r^2 = 0.207$, $F = 3.38$, df = 14, $P = 0.09$). A similar nonsignificant result was obtained for colony area changes between 2002 and 2003 ($r^2 = 0.028$, $F = 0.371$, df = 14, $P = 0.55$).

Discussion

Results of our study indicate that, under some conditions, reservoir species may be unimportant in maintaining sylvatic plague in an enzootic state in the prairie dog ecosystem and that some black-tailed prairie dogs may be enzootic hosts of the pathogen. First, an unexpected high percentage (57–63%) of prairie dog colonies tested positive for *Y. pestis*. Wide distribution and high prevalence of plague-positive fleas on FBIR was not an artifact of sampling because we collected fleas from dozens of colonies across a large geographic area (ca 50 km×80 km). Second, despite high prevalence of plague-positive fleas, there was no evidence of an ongoing epizootic, which would have been manifest in significant and consistent declines in the area of prairie dog colonies (Van Putten and Miller 1999; Cully and Williams 2001; Trudeau

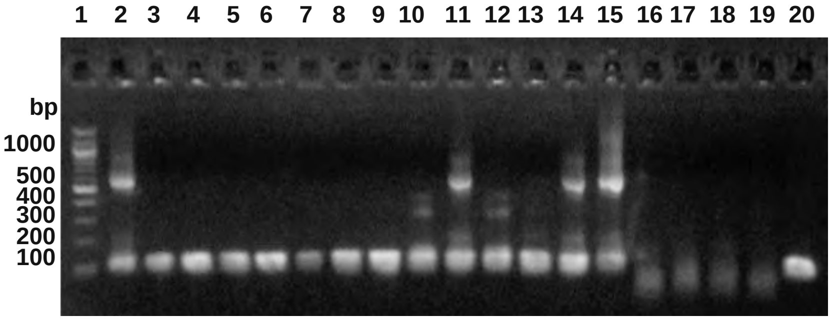

Fig. 1 Nested PCR results from selected flea samples. 1-μl samples were amplified as described in Materials and Methods; 5 μl each were electrophoresed on a 2% agarose gel. Lane 1: 100-bp ladder; Lanes 2–15: PCR-positive *Y. pestis* DNA; Lane 16: PCR-negative *Y. pestis* DNA; Lane 17: sterile water; Lane 18: *Y. pseudotuberculosis* DNA (10^{-3} diluted, representing ~8 × 104 CFU); Lane 19: *Y. enterocolitica* DNA (10^{-3} diluted, representing ~6.4 × 104 CFU); Lane 20: *Y. pestis* strain A1122 DNA (10^{-6} diluted, representing ~0.3 CFU)

Table 1 Sampling effort of flea collection and results of PCR-based sylvatic plague assays from black-tailed prairie dog colonies on the Fort Belknap Indian Reservation, Montana, 2002 and 2003. Results are mean ± SE

Year	Number of colonies sampled	Number of burrows sampled/colony	Number of fleas collected/colony	Number of fleas collected/burrow	Number of plague-positive colonies	Number of plague-positive burrows/colony
2002	48	10.9 ± 0.9	17.6 ± 1.9	1.5 ± 0.1	30	3.9 ± 0.5
2003	42	6.6 ± 0.6	8.5 ± 0.8	1.5 ± 0.1	24	2.3 ± 0.3

et al. 2004; Pauli et al. 2006). Prairie dog colonies fluctuated in size from 2001 to 2003, with some individual colonies both increasing and decreasing across years. Third, we collected fewer fleas from individual burrows than reported by previous studies which sampled fleas during ongoing epizootics (Lechleitner et al. 1968; Ubico et al. 1988; Cully et al. 2000). Low flea activity on FBIR provided further support that no epizootic occurred in 2002 and 2003. In sum, we failed to observe the widespread declines of colonies that would have been expected if reservoir species acted solely to maintain plague and if black-tailed prairie dogs were strictly an epizootic host.

Most studies implicate reservoir species as maintaining sylvatic plague in the prairie dog ecosystem between epizootics (Rayor 1985; Ubico et al. 1988; Menkens and Anderson 1991; Anderson and Williams 1997; Cully and Williams 2001). However, alternative mechanisms have been proposed for plague maintenance in other rodents and these mechanisms may pertain to black-tailed prairie dogs as well. For example, Keeling and Gilligan (2000) modeled plague persistence in rat metapopulations and reported that plague could exist enzootically even when 50% of the rat population was susceptible. Epizootics occurred when >80% of the rat population was susceptible. Enzootic maintenance of plague also occurs in Asian rodent populations such as great gerbils (*Rhombomys opimus*) where plague is native (Davis et al. 2004). These theoretical and empirical results suggest some parameters by which the disease can be maintained in an enzootic phase within a susceptible rodent host such as the black-tailed prairie dog (see also Webb et al. 2006). Black-tailed prairie dogs might also exhibit greater resistance to the disease than is currently believed (Pauli et al. 2006). Although sylvatic plague has been in North America for only 100 years, some degree of resistance could evolve within decades (Altizer et al. 2003). This possibility exists for black-tailed prairie dogs because populations typically harbor high levels of genetic diversity (Chesser 1983; Daley 1992; Altizer et al. 2003).

Poor vector to host transfer of the disease is also a possible explanation for the high level of plague found in fleas at our site. Different species of fleas have been shown to vary in their ability to transmit the disease, with the highest level of transmission seen with the rat flea *Xenopsylla cheopis* (Burroughs 1947; Holdenried 1952). *O. hirsuta* and *O. tuberculata cynomuris* are the most common fleas inhabiting black-tailed prairie dog burrows at our site and may be important vectors. Although their ability to transfer plague has not been extensively studied, recent evidence from Hinnebusch et al. (1998) indicates that *Y. pestis* may not replicate to high enough numbers in *O. hirsuta* to readily create the "blocked" condition required for transmission. These investigators observed that while 48% of *O. hirsuta* fleas collected from a prairie dog colony after a plague outbreak were positive for *Y. pestis*, <2% carried sufficient numbers of bacteria to be considered "blocked." This is consistent with our observation that larger numbers of fleas were PCR positive in this study

Table 2 Sampling effort of flea collection and results of PCR-based sylvatic plague assays from 15 intensively sampled black-tailed prairie dog colonies on the Fort Belknap Indian Reservation, Montana, 2002 and 2003. Results are mean ± SE

Sample period	Number of burrows sampled/colony	Number of fleas collected/colony	Number of fleas collected/burrow	Number of positive burrows/positive colony	Percentage positive burrows
May/June 2002	4.3 ± 0.5	10.6 ± 2.4	2.6 ± 0.5	1.0 ± 0.0	4.7
May/June 2003	3.3 ± 0.3	4.1 ± 0.5	1.3 ± 0.1	1.4 ± 0.3	28.0
June/July 2002	6.3 ± 0.9	8.8 ± 1.7	1.3 ± 0.1	3.7 ± 0.9	43.6
June/July 2003	3.1 ± 0.3	4.2 ± 0.8	1.5 ± 0.4	1.2 ± 0.2	12.8
July/August 2002	4.5 ± 0.5	5.3 ± 0.7	1.1 ± 0.04	1.7 ± 0.5	14.9
July/August 2003	1.9 ± 0.2	2.1 ± 0.3	1.0 ± 0.03	1.7 ± 0.2	34.5

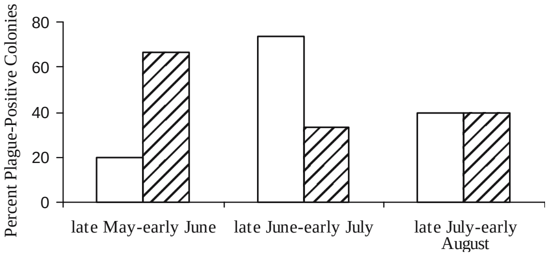

Fig. 2 Percentage of 15 black-tailed prairie dog colonies containing plague-positive fleas on the Fort Belknap Indian Reservation, Montana, 2002 (open bars) and 2003 (shaded bars)

than would have been predicted by the apparent overall health of the prairie dog colonies. Conditions under which transmission of plague begins are not understood but contributing factors likely include enhanced replication of *Y. pestis* in fleas (or higher levels of bacteremia in host animals, leading to uptake of more CFU in a blood meal [Hinnebusch et al. 1998]), greater flea infestation levels, and possible changes in susceptibility or resistance of the resident rodent population.

Although sylvatic plague did not appear to be intensifying or declining from 2001 to 2003 on FBIR, it appeared that some amplification had occurred seasonally. The late June/early July 2002 sample period showed a noticeable increase in the percentage of plague-positive burrows, whereas a similar increase occurred in late May/early June 2003. These effects were no longer apparent by late July/early August of both years. Thus, there may be as yet unknown seasonal factors that participate in the dynamics of plague at our study site.

Table 3 Area (ha) and percentage change in area of 15 intensively sampled black-tailed prairie dog colonies on the Fort Belknap Indian Reservation, Montana, 2001 to 2003

Colony	Area in 2001	Area in 2002	Percentage Change 2001 to 2002	Area in 2003	Percentage Change 2002 to 2003
85N	8	13	64	109	747
85W	30	16	–49	17	11
85WW	18	31	74	96	209
93	8	16	84	25	61
95	0	7	–	121	573
97S	4	26	515	3	–89
99	20	30	53	28	–9
99N	22	33	53	3	-90
100	52	100	91	17	83
101	14	40	186	8	–79
109	88	9	–89	84	796
111	48	34	–30	54	59
112	68	55	–19	56	2
126	17	4	–77	7	77
127	39	2	–95	3	33

Sylvatic plague is the only disease known to threaten black-tailed prairie dog populations with high mortality and local extirpation (Anderson et al. 1986; Miller et al.1994; Biggins and Kosoy 2001; Cully and Williams 2001; Pauli et al. 2006). *Y. pestis* is retained in the environment and can cause recurrent unpredictable epizootics, adding to the devastating nature of the disease on native biodiversity. The pathogen's reliance on reservoir hosts during enzootic periods is thought to be an important ecological aspect of the disease. Moreover, prairie dogs are thought to lack any immunity to the disease. Our highly sensitive PCR-based technique detected the pathogen in fleas collected from black-tailed prairie dog burrows during an enzootic phase. Thus, our technique could be used to screen currently healthy black-tailed prairie dog colonies that are being considered for black-footed ferret re-introductions and potentially to predict future plague epizootics in such colonies. Clearly, further basic research into the means by which sylvatic plague is maintained in the environment over enzootic periods is needed. Such research would also benefit conservation programs devoted to maintenance of black-tailed prairie dog populations and their habitat associates.

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References

Altizer A, Harvell D, Friedle E (2003) Rapid evolutionary dynamics and disease threats to biodiversity. Trends Ecol Evol 18:589–596

Anderson E, Forrest SC, Clark TW, Richardson L (1986) Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851. Gr Basin Nat Mem 8:11–62

Anderson SH, Williams ES (1997) Plague in a complex of white-tailed prairie dogs and associated small mammals in Wyoming. J Wildl Dis 33:720–732

Barnes AM (1982) Surveillance and control of bubonic plague in the United States. Symp Zool Soc Lond 50:237–270

Burroughs AL (1947) Sylvatic plague studies. The vector efficiency of nine species of fleas compared to *Xenopsylla cheopsis*. J Hyg 45:371–396

Biggins DE, Kosoy MY (2001) Influences of introduced plague on North American mammals: implications from ecology of plague in Asia. J Mammal 82:906–916

Chesser RK (1983) Genetic variability within and among colonies of the black-tailed prairie dog. Evolution 37:320–331

Cully JF Jr, Williams ES (2001) Interspecific comparisons of sylvatic plague in prairie dogs. J Mammal 82:894–905

Cully JF Jr, Carter LG, Gage KL (2000) New records of sylvatic plague in Kansas. J Wildl Dis 36:389–392

Daley JG (1992) Population reductions and genetic variability in black-tailed prairie dogs. J Wildl Manage 56:212–220

Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife: threats to biodiversity and human health. Science 287:443–449

Davis S, Begon M, De Bruyn L, Ageyev VS, Klassovskiy NL, Pole SB, Viljugrein H, Stenseth NC, Leirs H (2004) Predictive thresholds for plague in Kazakhstan. Science 304:736–738.

Engelthaler DM, Gage KL, Montenieri JA, Chu M, Carter LG (1999) PCR detection of *Yersinia pestis* in fleas: comparison with mouse inoculation. J Clin Microbiol 37:1980–1984

Faunawest Wildlife Consultants (1999) Status of the black and white-tailed prairie dogs in Montana. Montana Fish, Wildlife, and Parks, Helena, pp 1–28

Forrest S (2005) Getting the story right: a response to Vermeire and colleagues. BioScience 55:526–530

Gage KL, Kosoy MY (2005) Natural history of plague: perspectives from more than a century of research. Annu. Rev. Entomol., 50:505–528

Geoscience Associates (2003) Fort Belknap Indian Reservation mapping project

Hinnebusch JB, Schwan TG (1993) New method for plague surveillance using polymerase chain reaction to detect *Yersinia pestis* in fleas. J Clin Microbiol 31:1511–1514

Hinnebusch JB, Gage KL, Schwan TG (1998) Estimation of vector infectivity rates for plague by means of a standard curve-based competitive polymerase chain reaction method to quantify *Yersinia pestis* in fleas. Am J Trop Med Hyg 58:562–569

Holdenried R (1952) Sylvatic plague studies. VII. Plague transmission potentials of the fleas *Diamanus montanus* and *Polygenis gwyni* compared with *Xenopsylla cheopis*. J Infect Dis 90:131–140

Kartman L (1970) Historical and oecological observations of plague in the United States. Trop Geog Med 22:257–275

Keeling MJ, Gilligan CA (2000) Metapopulation dynamics of bubonic plague. Nature 407:903–906

Knowles CJ, Stoner CJ, Gieb SP (1982) Selective use of black-tailed prairie dog towns by mountain plovers. Condor 84:71–74

Kotliar NB, Baker BW, Whicker AD, Plumb G (1999) A critical review of assumptions about the prairie dog as a keystone species. Env Mgmt 24:177–192

Lechleitner RR, Kartman L, Golderberg MI, Hudson BW (1968) An epizootic of plague in Gunnison's prairie dogs (*Cynomys gunnisoni*) in south-central Colorado. Ecology 49:734–743

McCallum H, Dobson A (1995) Detecting disease and parasite threats to endangered species and ecosystems. Trends Ecol Evol 10:190–194

Menkens GE Jr, Anderson SH (1991) Population dynamics of white-tailed prairie dogs during an epizootic of sylvatic plague. J Mammal 72:328–331

Miller B, Reading R, Hoogland J, Clark T, Ceballos G, List R, Forrest S, Hanebury L, Manzano P, Pacheco J, Uresk D (2000) The role of prairie dogs as a keystone species: response to Stapp. Conserv Biol 14:318–321

Miller B, Ceballos G, Reading R (1994) The prairie dog and biotic diversity. Conserv Biol 8:677–681

Pauli JN, Buskirk SW, Williams ES, Edwards WH (2006) A plague epizootic in the black-tailed prairie dog (*Cynomys ludovicianus*). J Wildl Dis 42:74–80

Perry RD, Fetherston JD (1997) *Yersinia pestis*- etiologic agent of plague. Clin Microbiol Rev 10:35–66

Rayor LS (1985) Dynamics of a plague outbreak in Gunnison's prairie dog. J Mammal 66:194–196

Restani M, Rau LR, Flath DL (2001) Nesting ecology of burrowing owls occupying black-tailed prairie dog towns in southeastern Montana. J Raptor Res 35:296–303

Seery DB, Matiatos DJ (2000) Response of wintering buteos to plague epizootics in prairie dogs. West North Am Nat 60:420–425

Sodeinde OA, Goguen JD (1988) Genetic analysis of the 9.5-kilobase virulence plasmid of *Yersinia pestis*. Infec Immun 56:2743–2748

Thorne TE, Williams ES (1988) Disease and endangered species: the black-footed ferret as a recent example. Conserv Biol 2:1988

Trudeau KM, Britten HB, Restani M (2004) Sylvatic plague reduces genetic variability in black-tailed prairie dogs. J Wildl Dis 40:205–211

Ubico SR, Maupin GO, Fagerstone KA, McLean RG (1988) Plague epizootic in the white-tailed prairie dogs (*Cynomys leucurus*) of Meeteetse, Wyoming. J Wildl Dis 24:399–406

Van Putten M, Miller SD (1999) Prairie dogs: the case for listing. Wildl Soc Bull 27:1110–1120

Webb CT, Brooks CP, Gage KL, Antolin MF (2006) Classic Flea-borne transmission does not drive plague epizootics in prairie dogs. Proc Natl Acad Sci USA 103:6236–6241

Williams ES, Mills K, Kwiatkowski DR, Thorne ET, Boerger-Fields A 1994. Plague in a black-footed ferret (*Mustela nigripes*). J Wildl Dis 30:581–585

Woodroffe R (1999) Managing disease threats to wild mammals. Anim Cons 2:185–193

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THE BLACK FOOTED FERRET IN SOUTH DAKOTA

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The senior author, F. Robert Henderson, was a district game manager with the South Dakota Department of Game, Fish and Parks at Kadoka at the time of the study; he is now an extension specialist, Wildlife Damage Control, Kansas State University, Manhattan. Paul F. Springer was formerly leader of the South Dakota Cooperative Wildlife Research Unit, U. S. Bureau of Sport Fisheries and Wildlife, at Brookings. At present he is biologist-in-charge of the bureau's Migratory Bird Research Station, Arcata, California. Richard Adrian was a field assistant under the unit and now resides at Grosse Pointe Farms, Michigan.

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Figure 1. Adult female black-footed ferret in prairie dog town. Mellette County, South Dakota, July 1965. (Adrian)

INTRODUCTION AND PURPOSE

Since 1851, when the mammal shown in Figure 1 was first described as a separate species and named the black-footed ferret **(Mustela nigripes)** by naturalists John J. Audubon and John Bachman, it has remained hidden behind its mask. Speculation about its behavior patterns and life history has rarely been verified. In fact, human observation of the ferret was so infrequent that in 1964, when the U. S. Bureau of Sport Fisheries and Wildlife compiled its first published list of rare and endangered wildlife, the black-footed ferret was one of the species included.

Not only has the black-footed ferret been seen rarely, but it has been referred to in published material only incidentally. The principal literature on the species is limited to description of its physical appearance and habitat. No detailed or definitive studies on life history and ecological relationships are available. Little of the usual behavior which we observed has been reported in the literature, and some reports have proved to be in error. This leads to one inescapable conclusion — a scarcity of first-hand ferret observations in the past.

On August 7, 1964, while checking prairie dog colonies in Mellette County, South Dakota, William N. Pullins, district field assistant of the U. S. Bureau of Sport Fisheries and Wildlife, observed a black-footed ferret. Pullins was accompanied by the landowner's son, Richard Adrian. Subsequently, Adrian observed at least eight other ferrets in this town and in another 3 miles north.

Because of the unique opportunity to learn more about the black-footed ferret, arrangements were made for Adrian to begin regular observations of the animals under the auspices of the South Dakota Cooperative Wildlife Research Unit. These studies extended from August 17, 1964, through August 31, 1965. F. Robert Henderson made many additional observations throughout this and a subsequent period. Paul F. Springer supervised the over-all effort through June 1967, made observations, and helped to arrange for financial support by the Bureau of Sport Fisheries and Wildlife, the National Park Service, the Welder Wildlife Foundation, and the Badlands Natural History Association. Further field studies under the Cooperative Wildlife Research Unit were conducted from April 1966 to December 1967 and published separately by research assistant Conrad Hillman (1968).

Initially, the intent of the study was twofold: (1) to determine the distribution and status of the black-footed ferret in South Dakota, and (2) to gather information on its life history, behavior and ecology. As the study progressed, another objective was added: (3) to develop techniques for locating black-footed ferrets.

The present account records information gathered by the authors to June 1968. We believe this report of initial findings will be useful to others who want to learn more about this little known mammal. We hope this report will also be instrumental in encouraging more widespread and intensive investigation into the ecology and preservation of this elusive species.

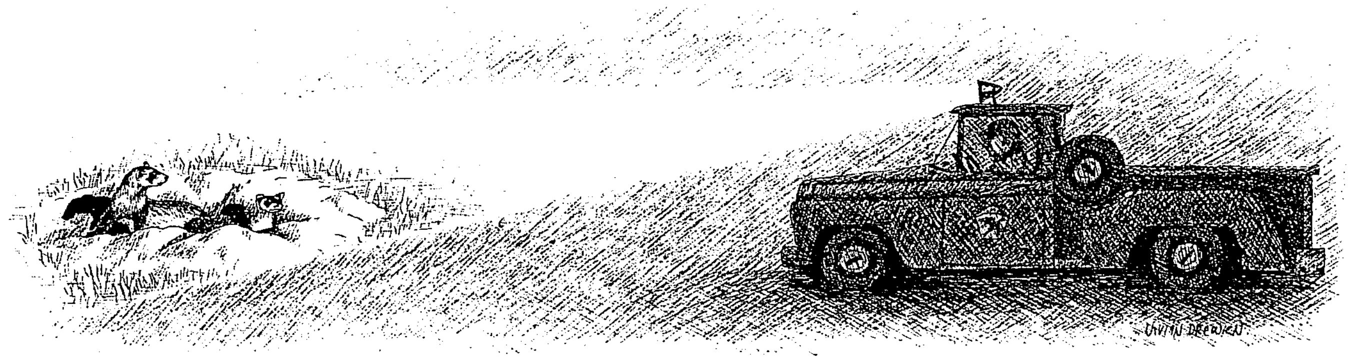

Figure 2. Observing ferrets at night with a spotlight.

METHODS

After the initial ferret sighting in August 1964, the two prairie dog towns were put under intensive surveillance both day and night. Observations were facilitated by the use of 7X binoculars and 15X spotting scope. Nocturnal observations were made by using several types of spotlights with various colored filters. The most effective was a 100-watt aircraft landing light mounted on top of a truck cab or placed in a portable navy signal light housing and plugged into a cigarette lighter socket (Figure 2). An army snooper-scope (Model IX) was also tested but found to be unsatisfactory because of low magnification and poor definition. Observations made in the field were recorded on magnetic tape or in notebooks and later transcribed to a journal.

In addition, several experiments on behavior, explained later in this report, were conducted at the study locations. All field observations were recorded in Standard Time.

In conjunction with its landowner game questionnaire the South Dakota Department of Game, Fish and Parks included a postcard with a color photograph of the black-footed ferret. These were sent to all ranchers in the state west of the Missouri River except Corson, Ziebach, Dewey and Stanley Counties. Information gained from this questionnaire aided in obtaining records of many additional black-footed ferrets. The cost of printing the postcard was paid for by the Badlands Natural History Association.

While conducting annual aerial antelope censuses and engaging in other activities, Department Game Division personnel plotted prairie dog towns on maps. Many of these towns were later visited by the authors in search of black-footed ferrets.

A thorough survey was made of published and unpublished literature on the black-footed ferret and the black-tailed prairie dog, with particular reference to South Dakota. In addition, all museums likely to have specimens of black-footed ferrets were visited or contacted, and examination was made of many of the specimens in their collections.

Throughout the report all county locations mentioned are in South Dakota unless otherwise indicated.

INDIAN RELATIONSHIP

Although a mystery to the white man, the black-footed ferret was known to the Plains Indian. According to the Sioux, their name for the ferret is "pispiza etopta sapa," meaning "black-faced prairie dog" (Vetal Romero and Leo Cadotte **pers. com.**). In the sign language of the Plains Indian the symbol for the ferret is Z. It is represented by an arm held up with elbow and wrist crooked. The person making the motion then points at something black and passes his hand across his face or holds up his hands (Ralph Hubbard **pers. com.**).

The ferret was also held in special regard by the Indian. In Montana the Blackfeet (Homolka 1964) and Cheyennes (Ralph Hubbard **pers. com.**) once used the tawny hides of the black-footed ferret as pendants on chiefs' headdresses. Peterson and Berg (1954) reported four black-footed ferret skins preserved in a collection of Indian relics at Pryor, Montana. The skins, which had been collected and stuffed by Crow Indians many years ago, were used in ceremonies. In the Indian museum at St. Francis, South Dakota, a collection of relics prepared by a Sioux to represent his native traditions includes two complete ferret skins in a display of sacred tribal objects. Leo Cadotte **(pers. com.)** points out that medicine men included ferret pelts among their medical paraphernalia as a symbol of influence when ministering to their patients.

There is no evidence that Indians have used ferrets in headdresses (Homolka 1964) or other ceremonial items for many years. Undoubtedly this is due in part to a general breakdown in Indian culture resulting from the formation of reservations.

Indians also had other uses for the ferret. A whole skin said to have come from the Sand Hills of Nebraska was used by Indians as a tobacco pouch (Vernon Bailey **unpubl. rept.**). Ferrets captured by Indians were reported to be eaten and considered a delicacy (H. H. Haecker **unpubl. rept.**).

The Pawnees of Nebraska knew the ferret as the "ground dog." They believed that if it sat up and looked at a person, meanwhile working its jaws as if chewing, the entrails of that person would at once be cut to pieces and he would die

(Grinnell 1895). The Sioux had various beliefs about the ferret. Some thought that anyone who killed a ferret would have bad luck (Vetal Romero **pers. com.**) or would be hypnotized (Leo Cadotte **pers. com.**). Others believed that a person would suffer no harm if he shot and killed a ferret, but would become ill if he missed or if he did not shoot (Bryan Provancial **pers. com.**). H. H. Sheldon (**unpubl. rept.**), writing in 1915, stated that ferrets in northern Shannon County were often killed by Indians.

PHYSICAL DESCRIPTION

The ferret was first described by Audubon and Bachman (1851) on the basis of an imperfect skin sent to them by naturalist Alexander Culbertson from the Fort Laramie, Wyoming, area (Hall and Kelson 1959). Subsequent collections have provided a more detailed description.

The most obvious distinguishing feature is the striking black mask across the face (Figure 1). The feet, legs to the shoulders and terminal fourth of the tail are also black. The remaining pelage is a pale yellow-buff becoming lighter on the under parts of the body and nearly white on the forehead, muzzle and throat. The top of the head and middle of the back are brown. The fur is short — about two-fifths of an inch in length on the back.

Young ferrets are lighter in color than are adults (Aldous 1940, Hillman 1968). We believe the pelage to be slightly paler in the male than in the female. We also observed in the field that most males have a black to black-brown longitudinal stripe in the pubic region, a characteristic that is faint or lacking in the females. This marking perimts field identification of sexes when the animals stand.

Springer checked this marking in the U. S. National Museum on 51 specimens that had been sexed (33 males and 18 females). The only exception from the rule were two specimens labelled male that did not have the stripe and one specimen labelled female that had a noticeable stripe. In the case of the males the stripe could have been sewed inside or trimmed off when the study skins were prepared.

Figure 3. Typical view of a black-footed ferret peering from a prairie dog burrow. Mellette County, South Dakota, July 28, 1966. (Rose)

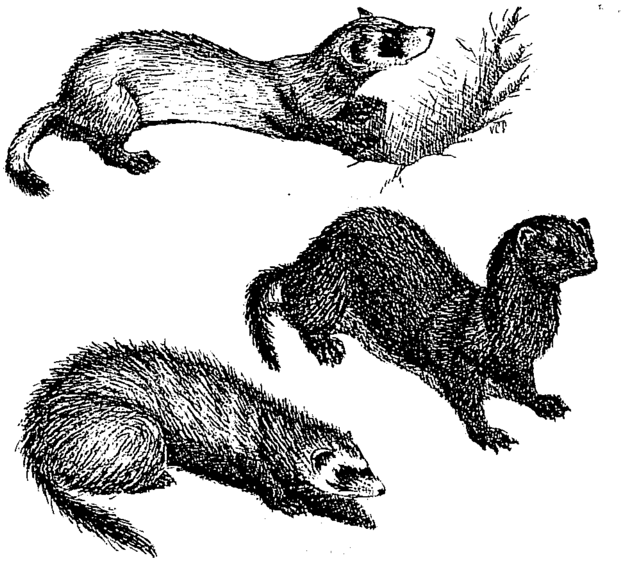

Figure 4. Black-footed ferret, mink and European fitch ferret.

Ferrets do not molt to a white coat in the winter as do some members of the genus **Mustela** in colder climates. Hall and Kelson (1959) state that the pelage may become slightly paler in winter. Our examination of museum specimens also indicates the winter pelage is slightly longer. The color of the ferret blends well with that of the soil in many prairie dog towns and may serve as a means of camouflage. Ferrets are most commonly observed peering out of a burrow with only their heads visible (Figures 2 and 3). In this posture the black mask obscures the form of the ferret and makes it difficult to distinguish. Probably the black mask has an additional function of reducing glare from light-colored soil or snow.

Ferrets are similar in size and weight to wild mink. Adult male ferrets are 21 to 23 inches in total length. Two males weighed 2 pounds 2 ounces and 2 pounds 6 ounces, respectively (Burt and Grossenheider 1964:62), and two females weighed 1 pound 11 ounces and 1 pound 14 ounces, respectively (see Page 36, records 212 and 215). A captive male varied in weight from 2 pounds, 11 ounces to 3 pounds, 3 ounces (D. R. Progulske **unpubl. MS.**).

Ferrets are short-legged, have long well-developed claws on the front paws, large ears and relatively large eyes. After dark the ferret's eyes show a green reflection in artificial light.

The native black-footed ferret should not be confused with the domestic European fitch ferret (Figure 4), which is descended from the European polecat. The domestic fitch ferret differs from the black-footed ferret in having longer and darker pelage on the back, yellowish underfur, and an entirely black tail. It was used for rodent control by the colonial settlers on their voyages across the Atlantic and has been employed for this purpose on farms. This is the animal that formerly was used for rabbit hunting. The domestic ferret rarely if ever becomes established in the wild.

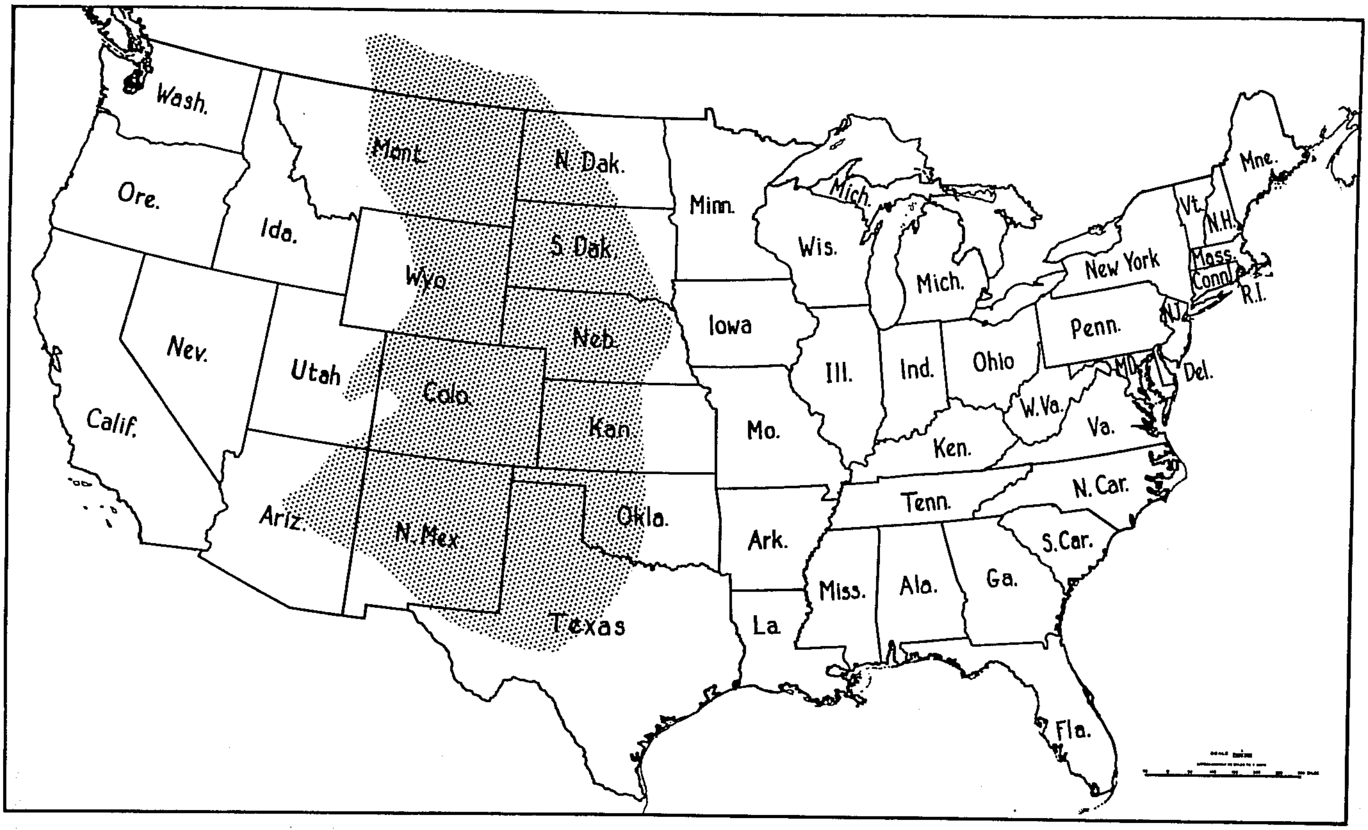

Figure 5. Former range of the black-footed ferret. (Hall and Kelson 1959)

HABITAT

The black-footed ferret is characteristic of the short and mid grass prairies, originally occurring from southern Alberta and Saskatchewan south to Arizona and Texas (Figure 5). Ferrets have been found living in haystacks, under buildings, and in ground squirrel colonies. The majority of evidence, however, indicates their principal natural habitat, at least in the northern part of their range, is prairie dog colonies. The historical geographic range of the black-footed ferret nearly coincided with the combined ranges of the black-tailed and white-tailed prairie dogs (Seton 1929, Burt and Grossenheider 1964).

The black-tailed prairie dog (Figure 6), the only species of prairie dog in South Dakota, lives in colonies or "towns." In the western part of the state these towns are typically on gentle slopes or level ground of clay and silt soils, primarily of the Chestnut zonal group. Average precipitation in this area varies from 13 to 19 inches annually (Westin et al. 1959). The grasses associated with this soil type are short grasses, including buffalo grass, blue grama, western wheatgrass, and green needlegrass, interspersed with patches of forbs. The burrow is the home of the prairie dog, and his feeding and digging activities favor the growth of forbs, many of which he eats (Figure 7). By cutting down these plants, prairie dogs provide themselves with a wide view. This enables them to scan the area for predators before leaving the protection of their burrows. Cutting down taller plants also favors the growth of short grasses, mainly buffalo grass and blue grama, which are among the staple foods of the prairie dog (Koford 1958).

Figure 6. Black-tailed prairie dogs at entrance of burrow. Shannon County, South Dakota, August 1966. (Henderson)

Figure 7. Prairie dogs feeding.

DISTRIBUTION AND STATUS

The ferret has never been considered a common species. Its secretive habits could also have contributed to this assumption. It is for these reasons, we believe, that the ferret was not described until 1851. During the next quarter century few specimens were collected for scientific study. Even today probably less than 200 specimens exist in museums.

The reasons for its lack of abundance are not fully known but may be partly an adaptation against overexploitation of its principal food, the prairie dog (Allen 1942). During the century following discovery of the ferret its reported distribution has decreased considerably from its maximum range, as evidenced by the results of a survey for the period 1946 to 1953 (Cahalane 1954). This decline appears to have been caused largely by changing land use and by man's determined efforts to poison the prairie dog. Thus, in areas where prairie dogs have been greatly reduced, the black-footed ferret is either extremely rare or no longer present. For example, 28 of 82 ferrets in the U. S. National Museum were collected in Kansas prior to the early 1900's (D. K. Fortenbery **pers. com.**). By the mid 1950's after intensive prairie dog control (Smith 1967), Hall (1955) considered the ferret to be very rare in that state. The ferret formerly was distributed in northern and central Texas (Seton 1929). In recent years the only reported records are of two specimens from the extreme northwest section in 1953 (Cahalane 1954) and 1963 (M. R. Evans **unpubl. rept.**). Cottam and Caroline (1965) point out that as a result of control, prairie dog populations today are but a small fraction of the numbers in Texas prior to 1915.

FINDINGS

Present Distribution and Status in South Dakota

During the study we gathered 82 records of actual specimens or of what we considered to be reliable sightings of ferrets in South Dakota for the period from August 7, 1964, through 1967. Only animals seen by us or qualified wildlife employees or by others whose reports were closely checked by us for veracity were included. Following is a summary of the records:

10 recovered specimens (mostly killed on roads)
6 sightings of 14 animals by authors
66 sightings of 94 animals by others
—
82 Total

These and subsequent records at the same sites represent 118 different ferrets, although some may have been the same individual at different locations. However an attempt was made to eliminate all duplicate records. Sightings at six of these locations involving 21 ferrets were made by Hillman (1968).

By contrast, records of 143 specimens or reliable sightings of one or more ferrets in South Dakota, altogether totalling 213 individuals, were obtained during the 75 years from the first report in 1889 to August 7, 1964. All the records from 1889 through 1967 are listed on pages 31-36.

In 1967, data based on aerial surveys and reports from district game managers of the South Dakota Department of Game, Fish and Parks

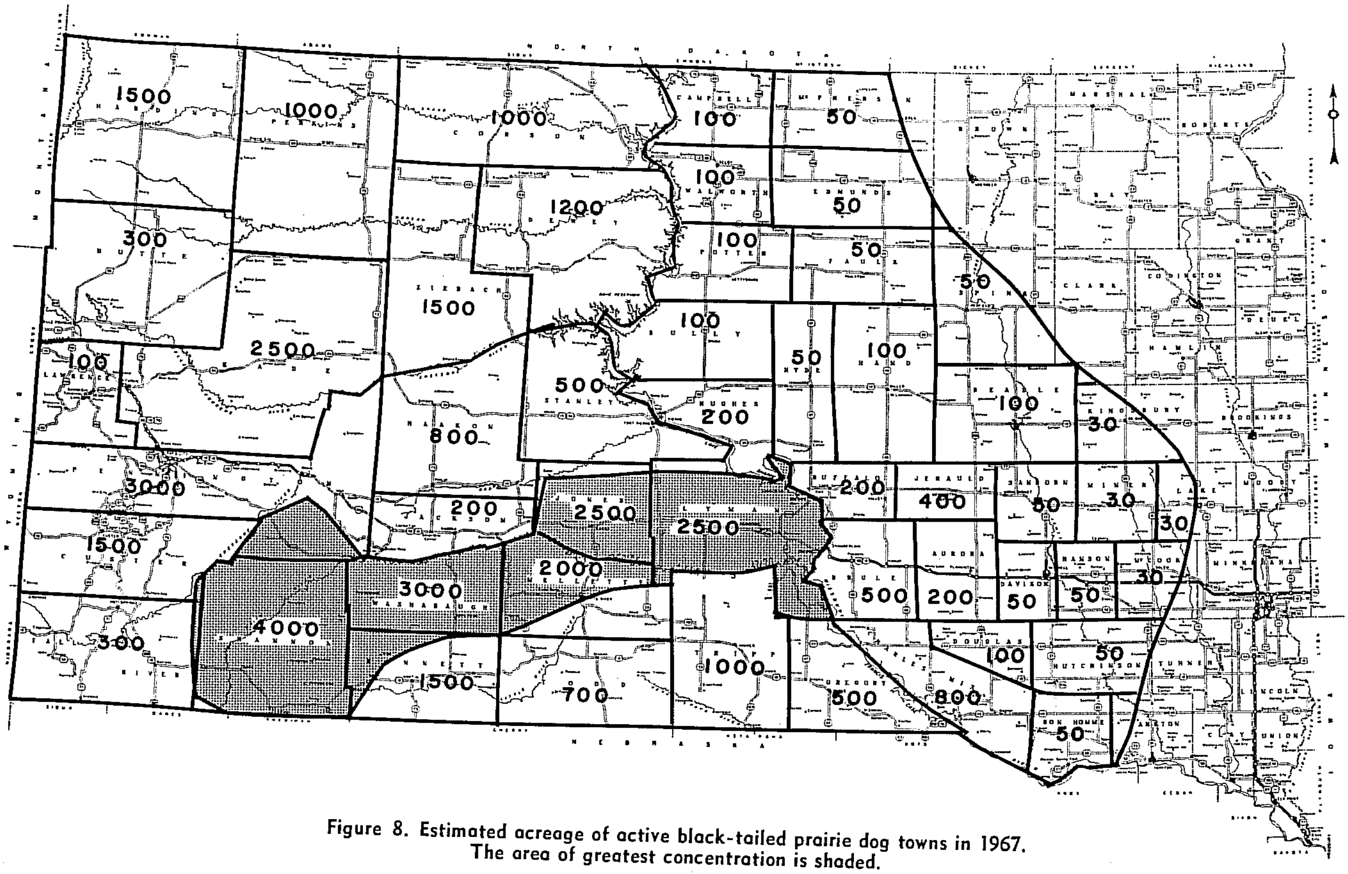

Figure 8. Estimated acreage of active black-tailed prairie dog towns in 1967. The area of greatest concentration is shaded.

showed that about 36,720 acres of black-tailed prairie dog colonies remained in the state. These towns averaged about 20 acres with a few large colonies covering 1,000 acres. The present range of the prairie dog and estimates of acreage by counties are shown in Figure 8. This agrees closely with the distribution shown by Seton (1929) and with an estimate by the Branch of Predator and Rodent Control (now Division of Wildlife Services) of the U. S. Bureau of Sport Fisheries and Wildlife of 32,991 acres of prairie dog colonies in 1961 (Presnall 1963). Very few ferrets were reported from counties east of those bordering the eastern side of the Missouri River and from the southwestern part of the state, areas in which there are few prairie dogs.

Life History

Summer: Family Activities

The black-footed ferrets initially sighted in August 1964 appeared to belong to two families. The animals located at the original site, a 300-acre prairie dog town in Mellette County, were identified as three ¾-grown young and an adult, presumably their mother. The other family, living in a 40-acre town 3 miles north of the original sightings, consisted of a litter of four ¾-grown young and presumably their mother. The following summer on July 13, 1965, another famliy of four nearly half-grown young and presumably their mother was observed on the town of the original sighting. Observations of family activities and photographs of young ferrets presented in this report are of all three families supplemented by observations and photographs of other ferrets from 1966 to 1968.

Additional family groups have been observed in summer. In July 1964, Frank Schramer, Jr., of Martin, South Dakota, told the authors of seeing a family of one adult ferret and four young cross a road at night near a prairie dog town in Washabaugh County. Another family of a female and five ¾-grown young was observed on July 29, 1966, by Conrad Hillman (1968) and Henderson in a Mellette County prairie dog town. Again, on July 10, 1967, Hillman (1968) and Henderson observed a female and four ⅓-grown young in another Mellette County prairie dog town Garst (1954 and **pers. com.**) and Cahalane (1954, Report No. 38) cite a record of an adult with a litter of four full-grown young in Haakon County on July 30, 1953. Cahalane (1954, Report No. 29) also cites a report of a litter of four young in a nest in a haystack in Perkins County in 1952. Lewis Bakken (**unpbl. rept.**) mentioned a female trapped on May 3, 1920, at Broadus, Montana, that was said to have been carrying 10 unborn young. Robert Schilder told us he saw eight ferrets in a Richardson ground squirrel colony in July 1965 in Faulk County. Warren (1942) mentioned nine ferrets having been seen together at one time in Colorado. From these observations it appears that four young are the rule, although litters of three and five or more may occur. The ferret has three pairs of mammary glands (Bailey 1926).

We never saw young in company with two adults, but Cahalane (1954, Report No. 35) cites an observation of two adults and one young together in early July 1953 in Ziebach County. Conversely, during the summer months young ferrets were never observed without being attended by one adult, presumably the mother. A male ferret may remain in the same general area where his young are reared, however. One male was seen near a female and her young in a prairie dog town in Mellette County by Hillman (1968) on August 25, 1966, a few days before the young ferrets left their mother. However, it is certain that the male ferret does not assist the female in rearing the young. The mother alone cared for them and directed their activities until they dispersed. In the early summer the mother was so secretive that, until the young were observed above ground in July, little was learned about their behavior. From her actions it was even difficult to determine which burrow contained the young.

The young rarely appeared during daylight hours. However, adult ferrets would often take advantage of the mid-morning sun's warmth to bask for several hours at a time near the crown of a burrow during the young-rearing period and afterwards in the fall and spring. D. R. Progulske **(per. com.)** noted that a captive ferret lay outside on sunny days, even during the winter.

Each night during the young-rearing period after the sun had set allowing darkness to shield the family's movements, the following drama would usually unfold. Upon digging her way out of her burrow if it had been covered by industrious prairie dogs during the day, the mother ferret would look around with only her head showing. At times she appeared to be sniffing the air. After several minutes she would emerge and cautiously canvass burrows in the immediate area. If she became alarmed, she would run with a rapid bounding gait to the nearest burrow. Often her head would reappear so quickly that it seemed a second animal was present. At times she would stand up on her hind legs, presumably to get a better view or scent (Figure 9). After her safety standard was satisfied, she would proceed to and dig open, if necessary, the burrow containing the young. Immediately thereafter she would enter. Almost always she would remain for 5 to 15 minutes before reappearing at the burrow opening to look about in all directions.


Figure 9. Adult female ferret standing up on hind legs. Mellette County, South Dakota, July 1965. (Adrian)

Gradually she would climb out of the burrow. Once out, she would run quickly from burrow to burrow, sometimes thrusting her head part way into the opening. At other times she entered a prairie dog burrow, quickly reappearing at the entrance, and darted to another burrow. Eventually she would return to the burrow containing the young. After entering she would remain for a short time before slowly emerging.

Finally the young would appear at the opening, first showing only their heads and gradually the foreparts of their bodies (Figure 10). Slowly, one by one, they would emerge from the burrow. If they were reluctant to leave the burrow, as they sometimes were, the mother would seize them individually by the nape and pull each one out (Figure 11). Frequently the mother would have to repeat this procedure several times before a young would remain outside. This shy behavior faded as the offspring grew in age and confidence. Then the mother was able to call the young out by uttering a repeated, low, plaintive **ungh** note.

Even after all the young had emerged from

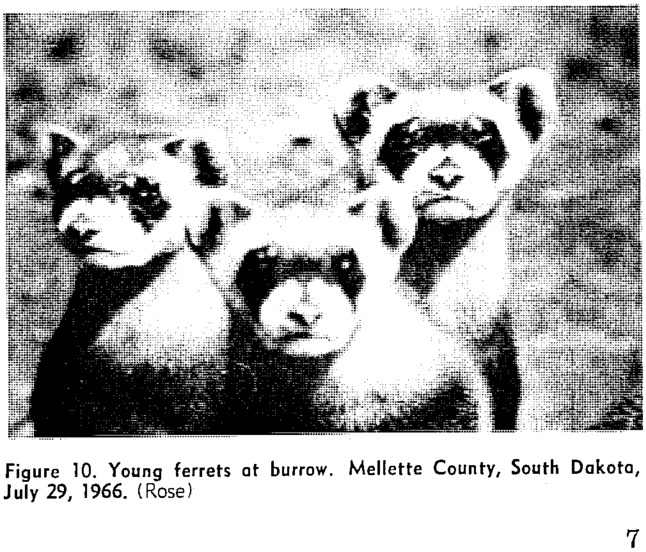
Figure 10. Young ferrets at burrow. Mellette County, South Dakota, July 29, 1966. (Rose)

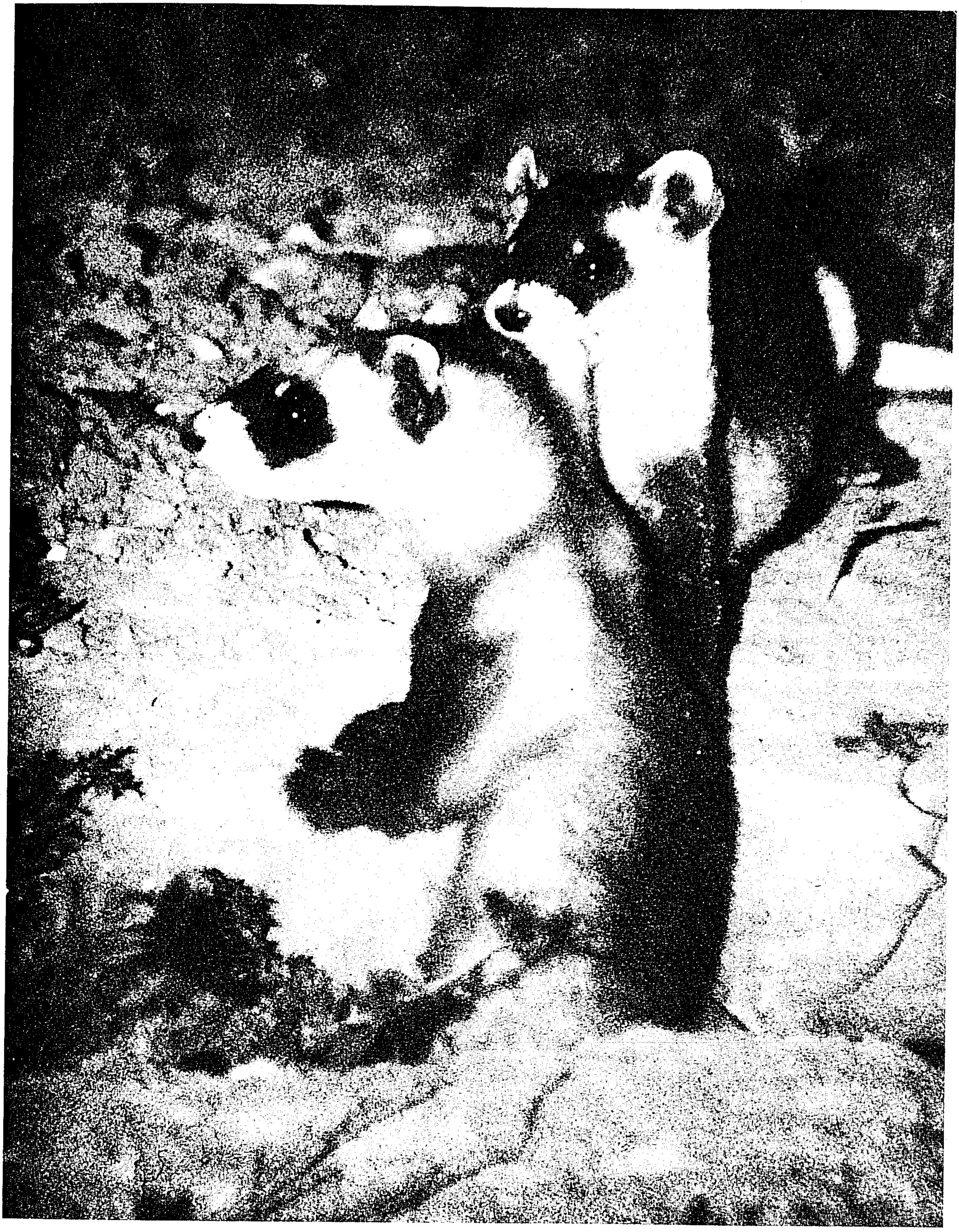

Figure 11. Adult female ferret pulling young from prairie dog burrow by nape. Mellette County, South Dakota, night of July 28, 1966.
(Rose)

the burrow, they hesitated to leave the immediate area. Sometimes they ventured a few feet away from the burrow and quickly darted back. Following the lead of the adult, however, they would eventually move to another burrow in single file with graceful agile bounds, creating the impression of a miniature train. Two of the young in the family observed in 1965 were smaller and more hesitant. However, they would join the mother and the two larger young when they started to move away from the burrow. Arriving at the burrow of the mother's choice, the young would enter after she had checked its safety. Again, she had to coax the reluctant offspring. Both Aldous (1940) and W. E. Garst **(pers. com.)** noted that ferrets they had in captivity were very cautious in new situations. Hillman (1968) observed that a mother ferret carried very young ferrets from one burrow to another.

After relocating her family, the mother again surveyed burrows, entering some, remaining out of sight for a few minutes, reappearing and finally staying down a burrow. Strecker (1910) reports similar behavior.

From June to the middle of July, the ferret family remained in the same general part of the prairie dog town. Around the middle of July, after the young were observed above ground at night, the family extended its area of activity and increased its frequency of relocation. We believe this modification in movement to be a response to both greater activity and food demands of the growing young and local decrease in prairie dogs through ferret predation.

By the middle of July the young ferrets, then nearly one-half adult size, were apparently being weaned as evidenced by an observation on July 16, 1965. When one of the young, having been coaxed out of the burrow by its mother, attempted to nurse, she pushed it away. At this time the mother was noticeably thin and unkempt from the demands of feeding and caring for the young. Her appearance contrasted with the fresh, sleek look of her offspring.

On July 27, 1966, Conrad Hillman (1968) observed an adult ferret, presumably a female, bring up a dead adult prairie dog from one burrow (Figure 12) and drag it to another burrow occupied by young ferrets (Figure 13). This "bringing home the groceries" was observed several times by the authors. Sometimes, however, it may be easier for the mother to lead the young to a below-ground dinner than to drag the food to them at home. For example, on the night of July 10, 1967, Hillman (1968) and Henderson watched an adult female drag three prairie dogs, one at a time, to a burrow. The next night the mother moved the young to this burrow where she had cached the dead prairie dogs. This behavior provides another reason for the increase in family travel after mid July.

Late summer and early fall: Family division and dispersion

By early August the mother ferret was separating the young, putting some in one burrow

Figure 12. Ferret bringing dead prairie dog out of burrow.

Figure 13. Adult female ferret with kill of adult prairie dog. Mellette County, South Dakota, July 28, 1966. (Rose)

and others in another. It was at this time that some of the young were first observed hunting occasionally at night by themselves. By mid-August they were seen during daylight hours, peering out of burrows, playing near the entrance and sometimes following their mother. The young ferrets were achieving their independence; they had advanced from shy, timid creatures to confident and inquisitive adolescents. The curiosity of both young and adult ferrets was displayed on several occasions when we successfully called animals from their burrows by imitating the coaxing sound made by the mother or by using a predator call to simulate the distress note of a rabbit. The young were still cautious, however, and would quickly retreat underground if the sound was too loud and harsh. Playing a recording of the alarm chatter (described later) of a captive individual evoked only mild interest from animals in the wild.

By late August or early September, when the young was as large as the adult, the ferret family started to disperse and was no longer seen as a closely knit group. However, on October 6, 1965, three animals were seen in close proximity on the 300 acre "south" town by Adrian and Springer.

Additional evidence suggests that the period from late summer through early fall is the principal time of dispersal. Altogether 43 per cent of the 70 ferrets found dead along roads or seen by casual observers outside of prairie dog towns were noted between mid August and mid October. Five specimens, (Pages 33-36, records 96, 107, 110, 204 and 224) could be aged and sexed. They consisted of three young males, one young female and one adult male. Age was determined by body weight and size, condition of gonads, conformation of baculum as noted in mink (Elder 1951) and amount of tooth wear.

In spite of fall dispersal a few animals inhabited the prairie dog towns under study as long as these sites remained suitable. Since ferrets were not marked for fear of disturbing them, the age and sex of these animals was not determined. The "south" town was inhabited by ferrets for at least 3½ years until the winter of 1966-67.

Some data show that ferrets will visit formerly used sites. In May 1965 Adrian excavated one burrow which the ferrets under observation in the 40-acre "north" town were known to have inhabited consistently during August 1964. The burrow angled downward at about 60° from horizontal for about 2 feet and then went straight down for 8 feet before leveling off horizontally. After excavation was terminated, the excavation was not filled in. Instead, boards were laid across at ground level to prevent cattle from falling into the opening. During the early morning of April 21, 1966, a ranch employee reported seeing a ferret enter the opening under the boards. On April 23, 1966, we inspected the burrow and found that a paper plug placed by Adrian in the burrow opening at the bottom of the 12-foot hole the previous year had been dug out by an animal. We supposed from the direction of the burrow that the remaining unexcavated portion led to another opening at ground level about 30 feet away. No further evidence of ferret activity was noted at the excavated burrow. Instances of ferrets visiting abandoned prairie dog towns have been reported by other investigators.

Late fall, winter, and spring: Sedentary existence and breeding

Observations of ferrets and their tracks showed that the animals were usually found singly during the late fall, winter and early spring, indicating that the young had achieved their independence. When two or more ferrets were observed to be active in the same prairie dog town during this period, they did not appear to associate with each other. At this time of year ferrets use a number of dens and may or may not favor certain ones.

As during the summer, activity was largely nocturnal, although more diurnal activity was noted in fall and spring than at other times of the year. Dartt (1879), W. E. Garst (**pers. com.**) and D. R. Progulske (**unpubl. MS.**) all noted that captive ferrets were most active at night.

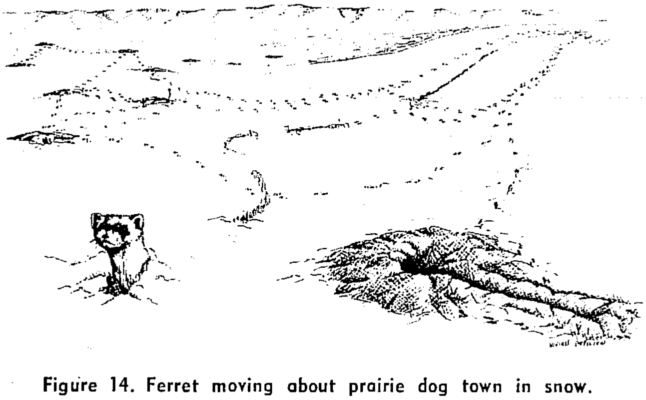

Figure 14. Ferret moving about prairie dog town in snow.

Tracking in the snow (Figure 14) showed that ferrets remained active through the winter, even when the outside temperature was as low as -18°F. A captive ferret did not hibernate but ventured out during sub-zero weather (D. R. Progulske **pers. com.**). Young (1946) states that the "ferret lays up throughout parts of the winter in some abandoned prairie-dog hole, or one it has appropriated to itself, until the weather moderates above ground."

The exact time of mating in black-footed ferrets in South Dakota is not known. By backdating from the estimated age of the young when first observed and using the 42-day gestation period of the closely related domestic fitch ferret (Bissonnette 1938), it is believed to be in April or May. Birth would be in May or June. An adult female ferret killed by a motor vehicle in Jones County on May 16, 1967, appeared to be in heat. Another female trapped May 3, 1920, at Broadus, Montana, was said to be carrying unborn young (Lewis Bakken, **unpubl. rept.**). A nursing female was collected on June 20, 1913, at Quinion, North Dakota (Bailey 1926), and young ferrets were reported in June in Billings County, North Dakota (Cahalane 1954, Report No. 22). A litter of ⅓-grown young ferrets observed by Hillman (1968 and **pers. com.**) on July 6, 1967 had their eyes only partially open. A ferret captured in Lyman County in August 1961 was thought to be less than 3 months old (D. R. Progulske **unpubl. MS.**).

Characteristics and Behavior

While engaged in family activities and later after achieving indepedence, the ferret exhibits the general characteristics and behavior patterns associated with typical life processes and features which constitute special adaptations of the species.

Senses:

The relatively large ears of the ferret (see Figure 15) suggest that its hearing is well developed. On one occasion Adrian tested the hearing ability of young ferrets. While observing them from a distance of about 5 feet, he scraped his foot across the floor of the truck. The young reacted almost instantaneously and ran down their burrow. On another occasion as a mother and young were being watched at night with a

Figure 15. Young ferret showing large eyes and ears. Mellette County, South Dakota, July 29, 1966. (Henderson)

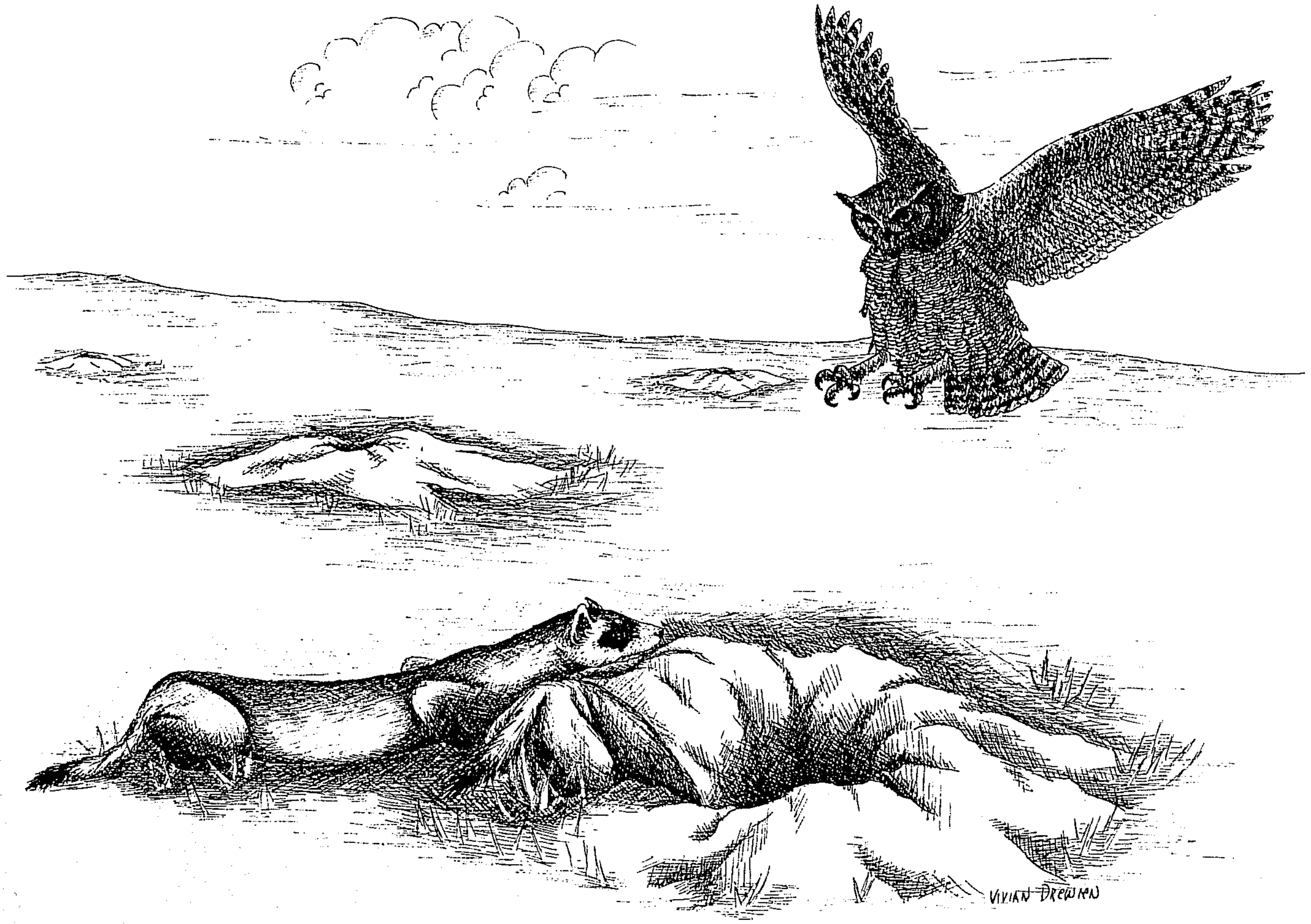

Figure 16. Great horned owl swooping on ferret.

light, they suddenly ran down their burrow about 7 feet away. Several seconds later a great horned owl swooped over the burrow entrance (Figure 16). It is believed the ferrets heard the owl. Twenty minutes later the young were playing above the ground again.

Smell also appears to be an important sense. Frequently the mother ferret would point her nose upward, apparently sniffing the air. Ferrets also seemed to rely on their sense of smell when nosing about burrow openings and when detecting dead prey put beside their burrows.

Sight is relied upon at close range but does not seem to be as important at distances over 300 feet. The ferret must be well adapated to seeing in poor light as they are active on dark nights when the moon is new.

Water requirements:

Ferrets were never seen drinking water, even though a creek and a few stock ponds and intermittently wet ponds were available on or near the several study areas. Water may be obtainable at the bottom of some prairie dog burrows. Proof that a black-footed ferret will drink water on occasion is provided by D. R. Progulske (**unpubl. MS.**) who observed that an animal he held captive drank water irregularly.

Fecal and urinary habits:

Only a few scats (fecal pellets) thought to have been deposited by ferrets were found. On October 14, 1964, Adrian observed a ferret drop the scat shown in Figure 17. It is suspected that ferrets deposit scats underground in a manner characteristic of weasels (Murie 1954). Presumed ferret scats collected from the surface of the ground had been deposited separately, usually near the burrow mound.

Ferrets urinate above ground at least some of the time. Urination sites at the opening of burrows were readily noticeable in the snow when

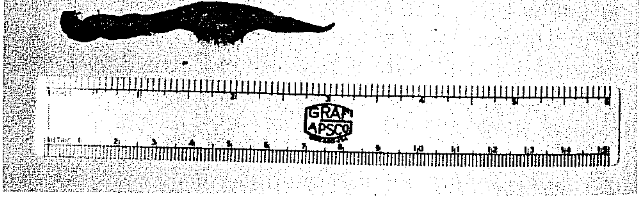

Figure 17. Scat dropped by a black-footed ferret. Mellette County, South Dakota, October 14, 1964. (Henderson)

ferret tracks were followed in the period from late December through March.

Aldous (1940), D. R. Progulske **(unpubl. MS.)** and W. E. Garst **(pers. com.)** noted that the ferrets they held in captivity made fecal and urinary deposits in one corner of their cages or sometimes in their den boxes. Garst's animal usually threw sand over the waste and sometimes dug a hole.

On the night of January 18, 1965, a stuffed ferret was placed at the entrance of a burrow which a ferret had entered. A few minutes later this ferret (sex unknown but believed to be a male) came out and investigated the stuffed ferret. Our subsequent examination showed that it had urinated on the board on which the stuffed ferret was mounted.

Odor:

Although we did not handle any live ferrets, we noted only a mild odor resembling that of a mink when we were in close proximity to disturbed individuals or when we examined dead animals. Hoffmeister (1963) states that the ferret has poorly developed scent glands, and Ralph Block **(unpubl. rept.)** did not note any odor. However, W. E. Garst **(pers. com.)** found that captive individuals he studied had an odor similar to that of a wet dog. This became more potent when the animals were disturbed. George Barnes **(unpubl. rept.)** observed that ferrets when aroused have a very disagreeable odor closely resembling that of a mink.

Play:

As do some other mammals, ferrets exhibited definite signs of play. Scuffling noises heard at burrow entrances during mid-July attested to the fact that the young were active and probably tussling inside their burrows. Above-ground observation confirmed their playful nature. On August 18, 1964, at 4:25 a.m., Adrian was watching two youngsters outside their burrow when one leaped up and executed a mid-air somersault. He also recored in his journal:

> "The two ferrets . . . seem to be playing. The ferrets can hop backward very fast. One just nipped the other one on the ear. . . . Both ferrets are playing; one stands still while the other jumps around. Then the first jumps at the second."

At times young ferrets appeared to be walking on their tiptoes. They also arched their back and tail and danced about. Aldous (1940) noted that a young captive ferret he raised liked to sneak up and grab a person's cuff or heel.

This playful spirit is not lost in the process of reaching maturity. During the winter Adrian found evidence of a slide in the snow made by a ferret (Figure 18). This individual had obviously

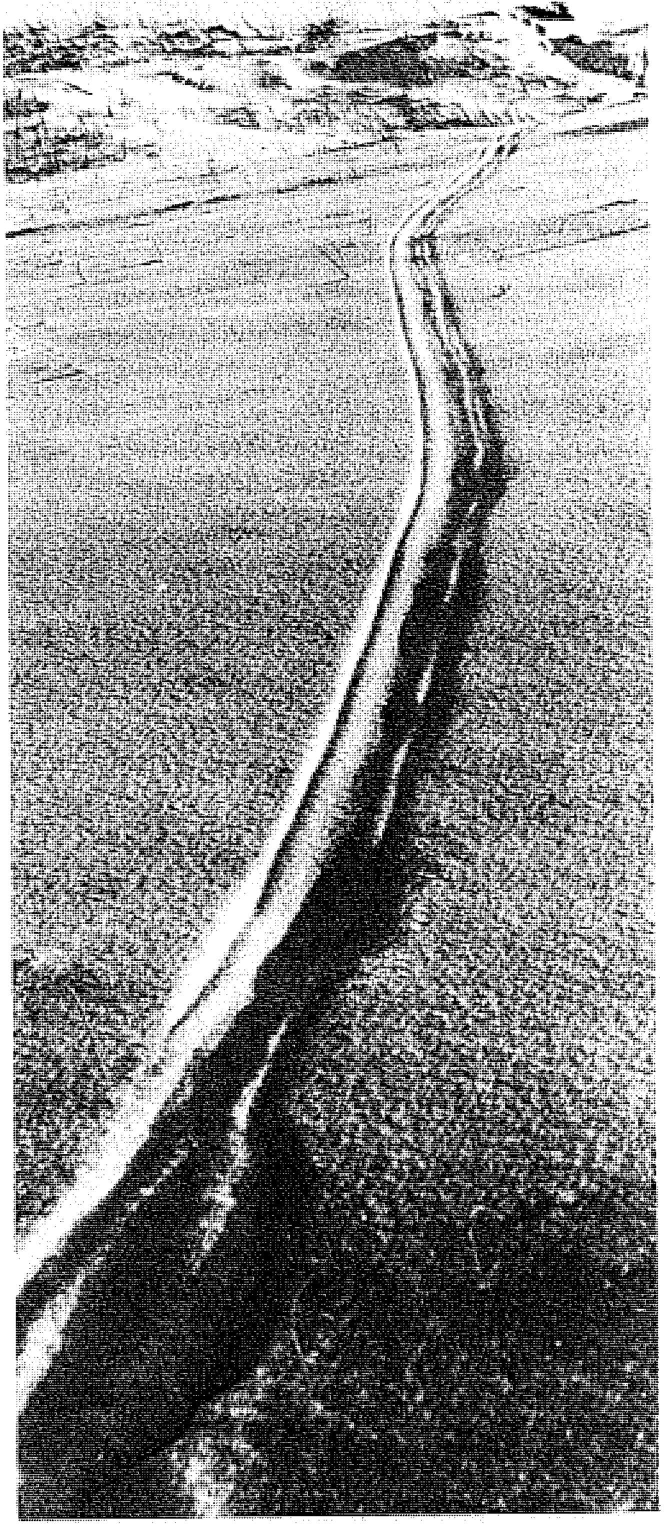

Figure 18. Ferret slide marks in snow on hill. Mellette County, South Dakota, January 1965. (Adrian)

Figure 19. Ferret signs: Tracks, front (above left) and hind (below left), and made when bounding (center); scats (right).

slid down the snow-covered hillside on its belly in much the same manner that a river otter slides down stream banks. Mink also have been found to slide down snow-covered slopes (Seton 1929, Marshall 1935). Ferrets tunnel under and through snow as do weasels (Seton 1929, Murie 1954). Adrian described this phenomenon in his journal on December 26, 1964:

> "At one part of the town where ferrets have been active, there was sign indicating where one animal had gone under the snow for about 6 feet before poking its head up and then continuing to tunnel through the snow." (Figure 14).

Tracks:

The hardness of the soil in western South Dakota prairie dog towns makes it difficult to find tracks left by ferrets. Therefore, most of the ferret tracks (Figure 19) were observed when snow covered the ground (Figure 14). Usually the distance between tracks in the normal bounding gait was 12 to 16 inches. One animal which was tracked in the snow appeared to have jumped 6 to 8 feet at times. Seton (1929) noted that the short-tailed weasel has been known to jump similar distances.

Identifying ferret tracks in fresh snow is complicated by their possible confusion with mink tracks, which are similar. On several occasions mink (Figure 4) were observed in the "south" prairie dog town in Mellette County, moving about in much the same manner as a ferret. At 10:30 a.m. on February 5, 1965, Adrian saw a mink going from burrow to burrow. Again on April 10, 1965, at 1:00 p.m. he wrote:

> "I saw a large mink in the central part of the town along the creek. It would make three or four bounds, stop, look around, and bound again. Soon it disappeared over the creek bank."

On April 22, 1965, at 7:30 a.m., Springer and Adrian checked the prairie dog town with binoculars and found many prairie dogs above ground. Adrian recorded:

> "Some were grazing; others were building up their burrows. In the north central part of the town, we saw several prairie dogs sitting stiffly and apparently alarmed. Investigation revealed a mink in the town. It was going in and out of burrows and apparently did not see us . . . Its paws and lower part of its body were wet from entering a small

Figure 20. Adult female ferret dragging dirt out of burrow. Mellette County, South Dakota July 28, 1966. (Rose)

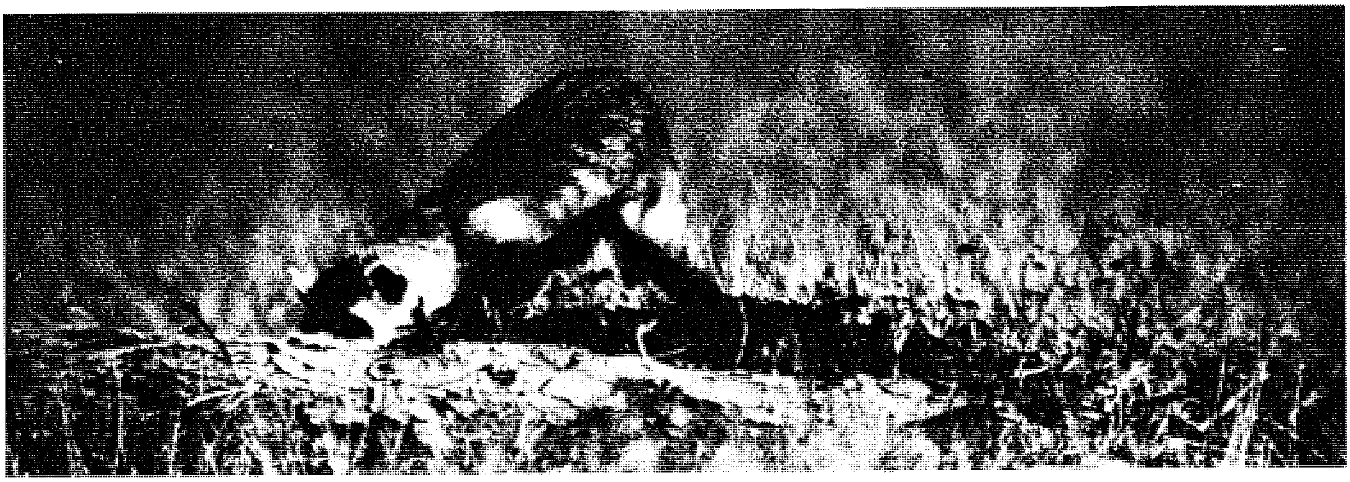

Figure 21. Ferret kicking dirt backwards after backing out of burrow in same path as on previous trips. Mellette County, South Dakota, July 28, 1966. (Rose)

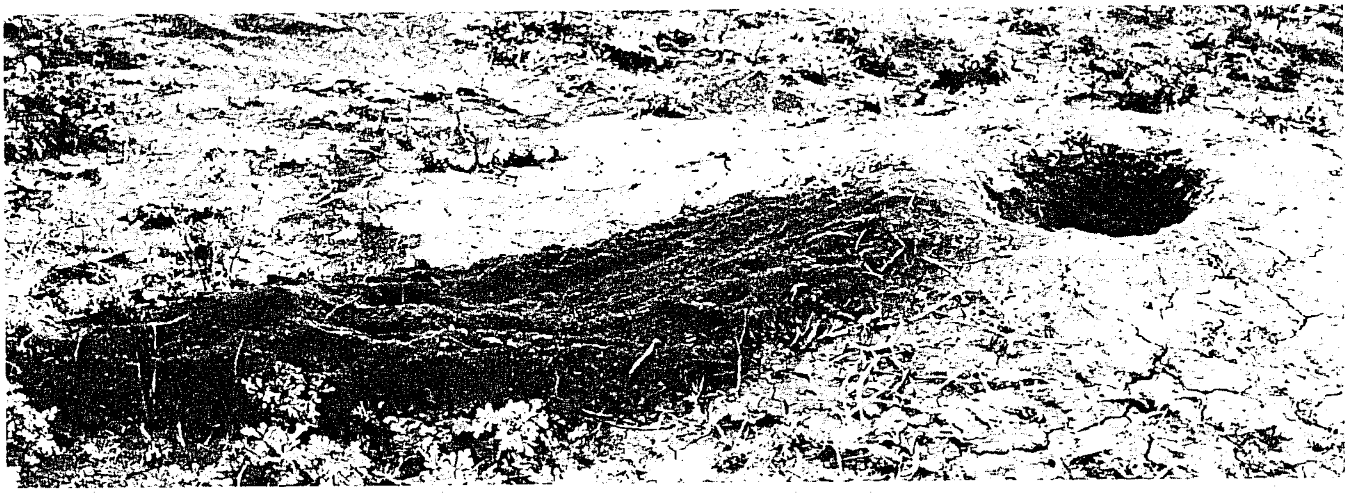

Figure 22. Characteristic trench made by ferret digging dirt out of prairie dog burrow. Mellette County, South Dakota, July 28, 1966. (Rose)

temporary pond. The mink then spotted us, but with the wind blowing toward us it was unable to determine what we were. It went hesitantly from burrow to burrow and when it had worked its way downwind, our scent reached it and it ran away to a prairie dog burrow about 200 feet away. It went down the burrow, came up and looked at us and went down again. Although we watched the burrow at a distance for about 15 minutes, it did not come out."

The mink and the ferret belong to the same genus; they are nearly the same size and to the human observer their tracks and scats are almost identical (Murie 1954). If mink are feeding on prairie dogs, their droppings probably would be similar to those of a ferret. It appears that where streams, stock ponds or other water areas are present nearby, mink are more frequent visitors to prairie dog towns than is generally realized. For this reason the possibility of the presence of mink should not be overlooked.

Digging:

As would be expected in an animal that spends much of its life underground in burrows, the ferret has well developed claws on its front feet — an adaptation for digging. When excavating in a burrow the ferret backs out with the dirt held against its chest with its front paws (Figures 20 and 21.) It generally comes out of the burrow on the same side. In each subsequent trip the animal drags the load of dirt a little further from the entrance, sometimes kicking it backwards. After repeated trips a trench from 3 to 5 inches wide and from 1 to 9 feet long is formed (Figures 22 to 24). Sometimes when only a small amount of dirt is removed, a trench is not formed. We noted that ferrets constructed trenches most often at night. A ferret observed by Springer and Adrian on the night of July 23, 1965, carried up a load of dirt about every 15 seconds. W. E. Garst **(pers. com.)** found that a captive ferret constructed a trench in cleaning out a burrow.

We consider trenching to be diagnostic of ferrets. No other animal we observed in a prairie dog town left a structure of this shape and size. The black-tailed prairie dog will excavate earth but generally this is deposited all around the burrow entrance to form a mound. Later it will build the mound higher by adding dirt from outside the mound. This direction of movement is just opposite that made by a ferret. In the spring of 1965 Floyd Vogelgesang told the senior author he saw a long-tailed weasel near a stock pond in Washabaugh County dig a trench similar to that of a ferret. However, the dimensions were 2 inches wide by 12 inches long. Mink on prairie dog towns have not been observed to dig.

White-tailed prairie dogs do not occur in South Dakota. Limited observation by the auth-

Figure 23. Good example of ferret trench. The observers are Richard Adrian (left) and Bill Pullins. Mellette County, South Dakota, January 20, 1965. (Kittams)

Figure 24. Old ferret trench as found after snow has melted and before weather warms. Prairie dog activity would erase this trench. Mellette County, South Dakota, March 1966. (Henderson)

ors of this species in Wyoming and Arizona indicates that the burrows are dug on more sloping ground than that occupied by black-tailed prairie dogs and that they tend to throw dirt out on the downhill side. This dirt is deposited in a broader but often shorter area than that by a ferret. No trenches suspected of being constructed by ferrets were observed in these white-tailed prairie dog towns.

Why the ferret digs at some burrows and not at others is not known. Since it commonly lives in prairie dog towns, it appears that the ferret ordinarily does not dig its own complete burrow system but instead appropriates that of a prairie dog, perhaps making some modification. Sometimes it digs to remove dirt thrown by prairie dogs down a burrow presently or recently occupied by a ferret, as described in the section on "Relationship to black-tailed prairie dog." At other times it probably digs to remove plugs of earth that prairie dogs construct inside their burrows to seal them off from the outside. R. R. Lechleitner **(pers. com.)** indicates the black-tailed prairie dog commonly plugs its burrow when it retires for the night or for extended periods.

We noted apparently more trenches in prairie dog towns in winter than in other seasons and relatively more in towns with a small prairie dog population than in those with large numbers of prairie dogs. Trenches probably are more evident in winter because at that time prairie dogs are less active, especially on non-sunny days. Thus, they do not erase the sign as quickly as they do during more active periods. Also, if the soil in the trench freezes, it cannot be easily disturbed by prairie dogs.

The repeated contact by a ferret dragging its long body at the crest of a burrow mound usually forms a smooth place (Figure 25). This characteristic was noted also by Garst **(pers. com.)**.

Another indication of ferret activity may be associated with its digging habits. In removing loose dirt from a burrow, the ferret may bring up hard dirt balls like those shown in Figure 26. These balls are formed of concentric layers of clay soil on which most prairie dog towns in western South Dakota are established. Commonly called Fort Pierre clay soil and locally referred to as "hard pan," this soil is normally more than 50 per cent clay. It is from a few inches to several feet in depth and usually on a layer of shale. The presence of dirt balls does not positively indicate ferret presence since they are found at a few burrows in nearly every prairie dog town sometime in the year. The balls, however, seem to vary more in size and in shape when located at

Figure 25. Ferret trench showing worn place near burrow crown. Mellette County, South Dakota, February 1966. (Henderson)

Figure 26. Dirt balls at burrow entrance. The nickel shows comparative size. Mellette County, South Dakota, July 23, 1965. (Springer)

ferret burrows then when found at prairie dog burrows. Although dirt balls are more frequent in wet weather, a few are present in dry periods at burrows that a ferret has chosen to frequent. Even though more investigation is needed to prove whether prairie dogs form most or all dirt balls, the occurrence of these structures at many ferret burrows makes them a potentially useful ferret indicator.

Ecological Relationships

Relationship to black-tailed prairie dog:

Dependence upon prairie dog. In a consideration of the intermammalian relationship of the black-footed ferret in South Dakota, the black-tailed prairie dog is a most important species. All indications vitally link the two animals.

The prairie dog's burrow provides a more moderate environment for the ferret when outside temperatures are high or low and during inclement weather. In one instance in June when the outside temperature was 128F. in the sun and 80 F. in the shade, it was only 53 F. at a depth of 8 feet in a prairie dog burrow. Wilcomb (1954) found the following temperatures during July and August: soil surface, 75 to 119 F.; air 6 feet above ground in shade, 73 to 90 F.; and air 41 to 49 inches below ground in a prairie dog burrow, 78 to 83 F. During January and February he recorded the following temperatures: soil surface, 24 to 66 F.; 6-foot elevation, 15 to 55 F.; and burrow at depth of 42 to 66 inches, 40 to 51 F.

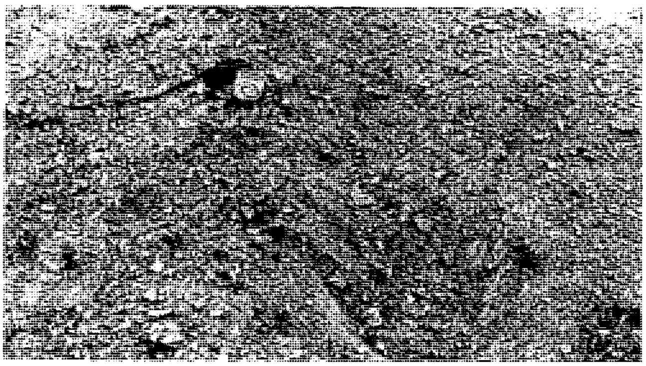

Figure 27. Ferret burrow covered by prairie dogs. Mellette County, South Dakota, October 1964. (Adrian)

There also seems to be little doubt that the prairie dog is the ferret's main food. This predator-prey relationship accounts for the ferret's titles of "prairie dog hunter" (Coues 1877), "prairie dog ferret" (Lantz 1905) or "king of the prairie dogs" (Vetal Romero **pers. com.**). Ferrets will consume items other than prairie dogs (see section on "Alternate sources of food") and have been observed away from prairie dog towns. However, they are most commonly seen in such towns, which suggests that these are their principal abode.

Examination of one known ferret dropping collected in a prairie dog town in Mellette County by Adrian as well as two droppings collected by Hillman (1968) showed that they consisted entirely of black-tailed prairie dog hair and bones. Prairie dogs were the predominant potential prey available to the ferrets. A prairie dog was found in the stomach of a ferret taken in Colorado (Coues 1877). The stomach of another ferret trapped in Pennington County in the summer of 1952 had only a grass seed which probably was taken incidentally (S. P. Young **unpubl. rept.**).

The 40-acre "north" town had about 167 active prairie dog burrows when the female ferret and four young were discovered in August 1964. By December 1964 only four active prairie dog burrows remained. This decline continued until the prairie dogs had completely disappeared by the spring of 1965. In the spring of 1966 many thirteen-lined ground squirrels, a species which previously had been uncommon in the town, were observed using the abandoned prairie dog burrows as well as their own burrows.

The 300-acre "south" town experienced a similar decline from approximately 1200 active burrows in the fall of 1964 to only about 20 in the spring of 1966. No prairie dogs remained in the spring of 1967.

Plague, a disease transmitted by fleas, is known to decimate prairie dogs at times. Prairie dog fleas were collected from several animals in the small town during the fall of 1965 and submitted to the Plague Laboratory, Communicable Disease Center, San Francisco, California. These fleas were reported not to be carrying plague bacilli. The possibility of other disease was not investigated, but there was no above-ground evidence of mortality induced by pathogens.

Investigation of a number of other towns in Mellette County disclosed that prairie dogs had disappeared in four of them without having been poisoned by man. Ferret sign, mostly old and consisting of trenches, was present in all four. These plus the "north" and "south" towns all occurred in a 3 x 6 mile area. Five other towns in this same area did not decrease in size during this period and repeated investigation showed an absence of ferret sign.

Thus, from the evidence collected, it appears that ferrets, and other predators, may assist in the depopulation of some prairie dog towns. A number of old reports exist in which ferrets are said to have greatly diminished or exterminated prairie dogs in a town (Roosevelt 1900, Lantz 1905, McCandless 1908, J. W. Glessner **unpubl. rept.**, A. E. Oman **unpubl. rept.**, S. W. Glenn **unpubl. rept.**, S. P. Young **unpubl. rept.**).

It is noteworthy that when a ferret is active on a prairie dog town during the day the prairie dogs remain above ground. In spite of all the time spent in observing ferret behavior, a ferret has been witnessed actually killing a prairie dog above ground only once (Hillman 1968). Apparently, prairie dogs are more secure from ferrets here than in their burrows. Conversely, when larger predators, such as a badger, coyote, or man, that cannot readily pursue prairie dogs down their burrows, appear on a town, the prairie dogs seek refuge below ground. From this we conclude that the major portion of actual killing of prairie dogs by ferrets occurs underground, probably at night when prairie dogs have retired to their burrows and ferrets are active. An exception to nighttime feeding may be during the day when adult prairie dogs are on the surface and when young prairie dogs that are in their burrows are easy prey for ferrets.

Springer did find a dead prairie dog, its throat cut, at the crown of a burrow on the night of October 6, 1964, in the 300-acre "south" town in Mellette County. When he came on the town after dark at 7:15 p.m., he noted a ferret. As he approached, it moved off and circled part of the town, returning to the original site. At this time Springer first noted the dead prairie dog. When he approached the ferret again, it partly descended the burrow. While Springer was taking pictures, it seized the prairie dog and dragged it into the burrow. Then it proceeded to consume it for 30 minutes in a chamber about 4 feet under ground. Springer could see part of the ferret and hear it eating. Afterwards it came out of the burrow and descended into another one. Eleven hours later Springer and Adrian dug out the burrow but found no trace of the prairie dog. The burrow ended in the chamber, although examination showed that a tunnel leading further down had been blocked off some time previously.

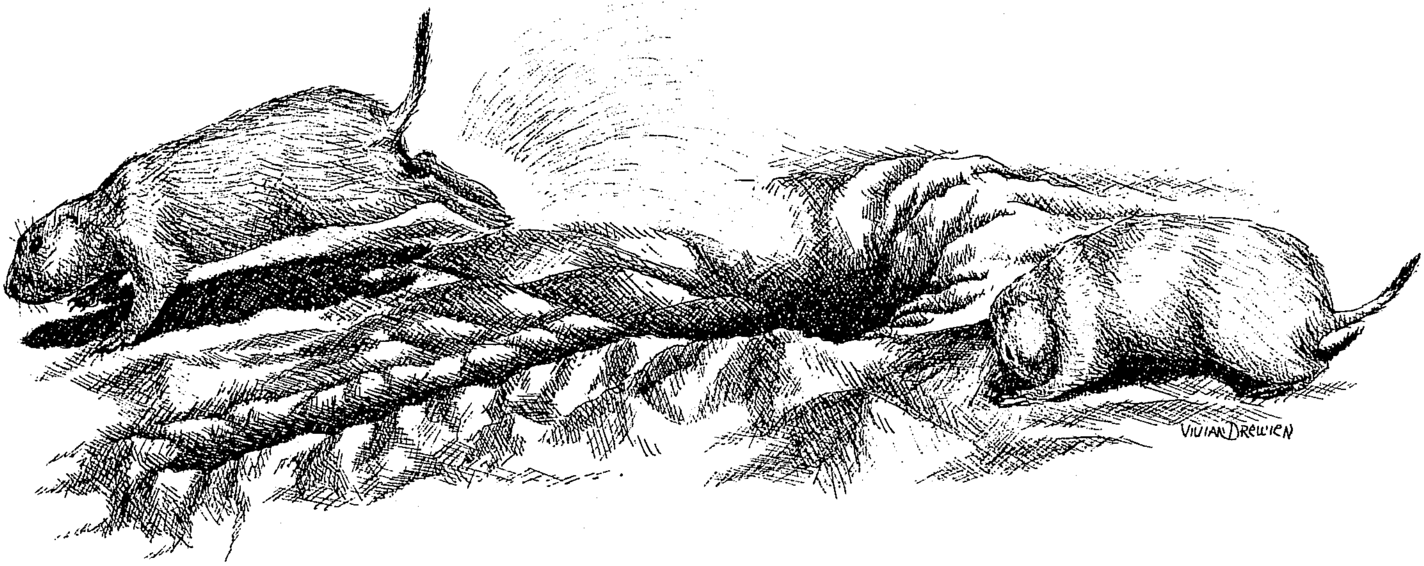

Figure 28. Prairie dogs covering burrow occupied by a ferret.

A recently killed prairie dog, again with its throat cut, was reported to Adrian by Clarence Krogman on March 3, 1965. It was at the entrance to a burrow in a prairie dog town in Mellette County that was being poisoned with strychnine-coated oats. Two days later Adrian observed ferret tracks and dirt trenches in the snow. Lantz (1905) mentions that an occasional dead prairie dog with its throat cut is found outside a burrow.

It seems likely in the above instances that the ferret either chased the prairie dogs up to the surface where it dispatched them or killed them underground and brought them up to the surface.

In December 1964, Adrian found many ferret tracks at the snow-covered 300-acre "south" study location. Near one burrow which had been recently dug out by a ferret, he found a black-

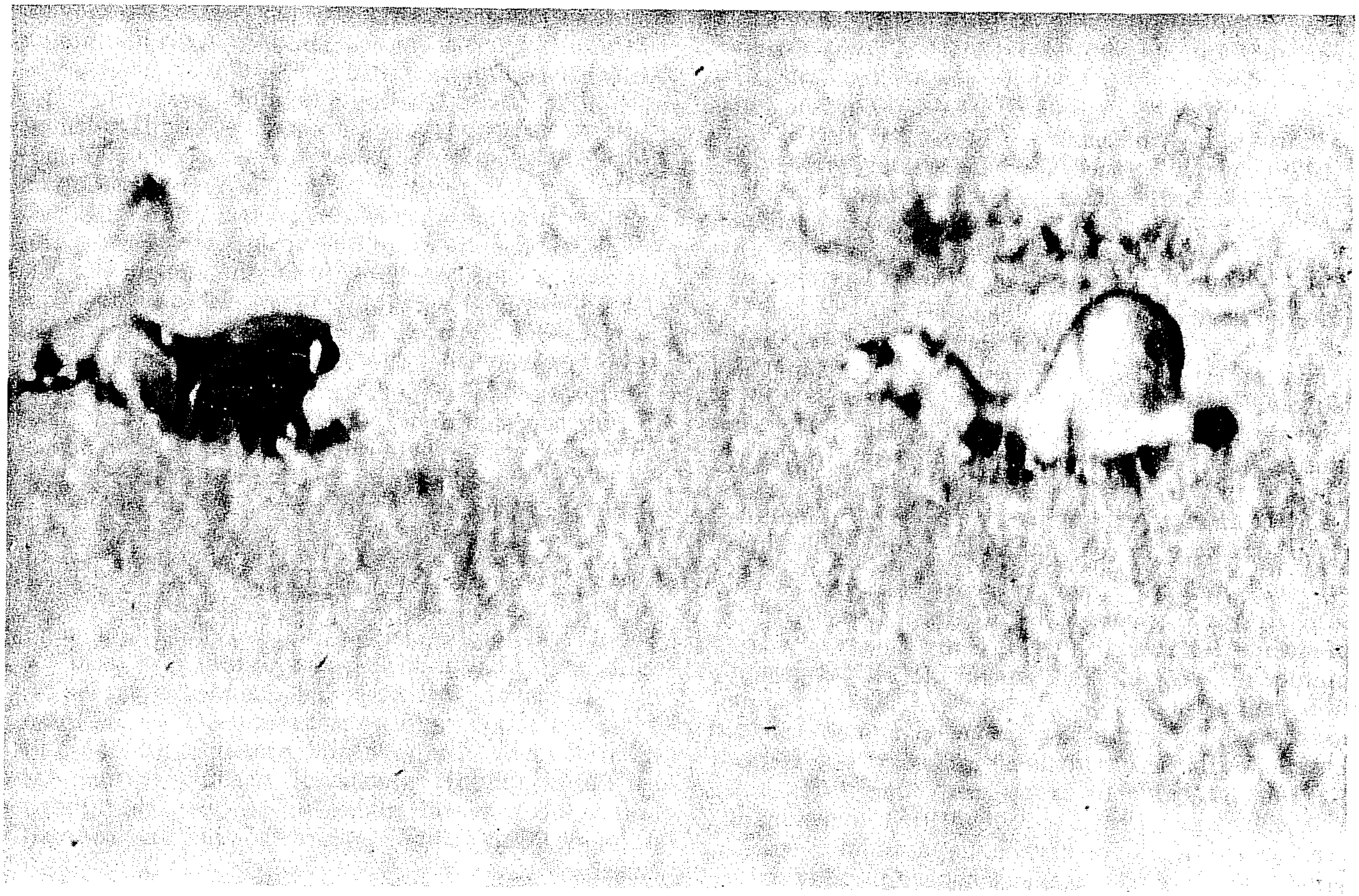

Figure 29. Black-tailed prairie dog running in front of black-footed ferret. Mellette County, South Dakota, August 1964. (Rose)

proached that burrow and made darting movements toward the ferret from about 2 feet. Whenever the ferret backed down the burrow, the prairie dog dug furiously in an effort to cover the burrow opening. Subsequently, the ferret ran to a nearby burrow and descended it.

On a number of other occasions prairie dogs were seen running in front of a ferret as if to divert it or confuse it (Figure 29). Although prairie dogs will intimidate a ferret and sometimes cause it to return to its burrow, close observation showed that the prairie dogs would usually give way to a ferret if it persisted in its course of action. Prairie dogs closely followed a ferret moving about a town and seemed to be chasing it but always fell back when the ferret turned and faced or chased them. Mead (1885) recorded similar observations. At times it appeared that a ferret would retreat in order to lure the prairie dogs to a point where the ferret would chase one of them. In the few instances where a ferret was forced to withdraw, it was believed to be a younger, less experienced animal.

At times a ferret may be injured by a prairie dog. In August 1965 the mother ferret on the "south" town incurred a large cut that ran from her forehead down between her eyes. She did not have this cut when observed previously. The injury, however, did not seem to interfere with her vision or to be infected. However, she often scratched the scab with her hind paw. Possibly this wound was inflicted in an encounter with a prairie dog or one of the animals described in the section on enemies. D. R. Progulske **(unpubl. MS.)** witnessed a fight in which a prairie dog bit a captive ferret on the side of the face and shoulder before the ferret killed it.

Although prairie dogs ordinarily cannot kill a ferret they will if the situation permits. Support for this statement is based upon a report of a ferret caught in a trap in Kansas. This animal was attacked and killed by a small group of prairie dogs. (Kellogg 1960).

Relationship to other animals:

Alternate sources of food. The fact that black-footed ferrets have been found living in haystacks and alfalfa fields, around buildings and in proximity to other animals besides prairie dogs indicates that they can subsist, for a while at least, without these rodents. It is not known, however, if they can maintain such a livelihood indefinitely.

K. E. Christiansen informed W. H. Kittams **(unpubl. rept.)** that he saw several ferrets come out of a haystack which was being moved on a ranch in Lyman County in 1964. P. W. Kattenbach, a Washabaugh County rancher, told us he saw a black-footed ferret in an oats strawstack in the late winter and early spring of 1966. He reported that this stack harbored many mice in early winter but that very few remained by late spring. Cahalane (1954-Report No. 29) mentions a nest of four young ferrets in a haystack in Perkins County, and Anthony (1937) states they hunt field mice. William Hespe told us he had a close view of a ferret in a haystack in Haakon County on April 15, 1965. Our investigation the next day failed to reveal any invidence of its continued presence, and Hespe did not see the ferret again. Dono Capp **(pers. com.)** killed a ferret in a haystack in Ziebach County in January 1958, and Russell Allard **(pers. com.)** observed a ferret under a haystack in Washabaugh County in June 1965.

A ferret was caught by a farmer in a rat trap near some farm buildings in Sully County in the summer of 1959 and released (W. H. Kittams **unpubl. rept.**), and a family of ferrets used some deserted sheep sheds as a home (Grinnell 1896). Mrs. John Larsen told us she observed a ferret in some old culverts in a farmyard in Haakon County in April 1965. Nelson (1918) mentions a ferret that stayed for several days under a wooden sidewalk in Hays, Kansas, where it killed rats living there.

On the morning of August 28, 1964, Adrian watched a ferret leave its burrow and chase a thirteen-lined ground squirrel. Two other ferrets emerged from the burrow and joined the chase. The ground squirrel escaped by going down its burrow which was too small for its pursuers to enter. The three ferrets then returned to their burrow. Loras Riggins told us he saw a ferret catch a thirteen-lined ground squirrel in an alfalfa field in Washabaugh County in the summer of 1962. Cahalane (1954-Report No. 16) recorded a ferret seen carrying a thirteen-lined ground squirrel in a prairie dog town, and Roosevelt (1900) mentions they feed on gophers.

Robert Schilder informed us he saw a group of eight black-footed ferrets in a colony of Richardson ground squirrels in Faulk County for a few days in July 1965. H. G. Troester reported to us that he saw a ferret cross a highway in mixed cropland, hayland and pasture near Dawson, N. D. on June 18, 1963. Richardson ground squirrels were present within a mile or so, but prairie dogs are not known to occur nearer than 50 miles west.

Adrian's notes for October 14, 1964, describe an experiment with a desert cottontail. Adrian noticed that a number of prairie dogs were sitting up on their burrow mounds with their attention directed toward a ferret that was looking out of a burrow. After watching the ferret travel from burrow to burrow, Adrian and a companion moved to the last burrow into which the ferret had gone. Adrian's companion thrust a live cottontail with a 10-pound-test fish line attached, down the burrow and held it there for about a minute. When he pulled it out, the rabbit's throat was cut and it showed little sign of life. The ferret stuck its head out of the burrow and peered at the observers for a couple of minutes. Its whiskers were noticeably bloody. The ferret then came out of the burrow and ran into another about 40 yards away. When it went down this burrow, Adrian's companion lowered the rabbit after it again and left it there for about 3 minutes. When he tried to pull the rabbit out, the fish line broke as the ferret apparently held onto the rabbit. By placing his ear at the mouth of the burrow, Adrian could hear the ferret eating the rabbit.

R. W. Gerhardt **(pers. com.)** observed a ferret chase a cottontail down a sheepherder's trail on the afternoon of August 22, 1963, in Carbon County, Wyoming. Roosevelt (1900) lists sage rabbits (probably desert cottontails) and jackrabbits (probably white-tailed jackrabbits) as a source of food, and rabbits and hares are also mentioned by Audubon and Bachman (1851) and by Lantz (1905). Roosevelt (1900) cites an instance of a ferret attacking a fawn pronghorn antelope, but this appears to be an unusual case.

Birds also seem to attract the ferret's attention, perhaps appealing to its curiosity as well as to its predatory nature. On August 23, 1964, Adrian saw a ferret leave its burrow and lie beside the entrance for a minute or so, watching a western meadowlark. It then chased the bird, which flew away. A horned lark landed near the burrow entrance and the ferret chased it. On other occasions a western meadowlark swooped overhead at a ferret, and a killdeer put on a broken-wing act. Both apparently recognized the ferret as an enemy. Baker (1889) states that the ferret makes occasional raids on poultry, and Mrs. Harry Roth told us of a ferret killing chickens in her chicken house near Reliance. The ferret is said to feed on ground roosting birds at night and on burrowing owls in their holes as well as to climb low trees in desert regions to rifle nests or pounce upon roosting birds (Olin 1959). Audubon and Bachman (1851), Roosevelt (1900) and Anthony (1937) also mention birds and their eggs as items in the ferret's diet.

Hollis Young told us he saw a ferret carrying a snake into a prairie dog burrow in Jackson County in May 1965. Small reptiles and snakes are mentioned by Audubon and Bachman (1851) and by Roosevelt (1900) as food items of ferrets.

Ralph Hubbard **(pers. com.)** observed a ferret batting down and eating moths under a street light in Wheatland, Wyoming in 1931 and saw a ferret eating Carolina locusts at Elbert, Colorado, in about 1927. We watched ferrets, particularly young, catch flies in their mouth. This habit has also been reported by George Barnes (**vide** W. E. Garst **pers. com.**).

Although ferrets have been known to live for a time on these other sources of food, they apparently will not do so indefinitely. We spent many hours making biological observations in a variety of habitats other than prairie dog towns. Never once did we see a ferret or its sign even though we were in the known geographic range of the species. We also checked 42 reports by others of ferrets 1 to 5 miles from known prairie dog towns. Although we were satisfied that these people had actually seen a ferret, our observation of the areas and the surrounding vicinity failed to produce a sighting or sign of an animal. From this we conclude that these ferrets were occupying the areas only temporarily. This is further supported by the fact that most of these records occurred in the fall when our studies show ferrets are most apt to be on the move.

A considerable number of people in western South Dakota trap fur-bearing animals, mainly mink. If ferrets were numerous outside of prairie dog towns, presumably some would be caught. Such, however, is not the case.

It should be noted, too, that many of the alternate kinds of food observed to have been consumed by ferrets are not available to them in winter on the northern plains. At that critical period the black-tailed prairie dog remains as the most abundant and readily secured food item.

Enemies. Observations indicate the ferret has several important enemies. One possibly formidable threat, however, was shown to be viewed with seeming indifference. It might be expected that the presence of man would be alarming to this secretive animal. Instead, the authors were amazed at the lack of fear by ferrets, particularly adults, toward humans. In fact, ferrets were quite confiding and curious in their behavior.

When approached closely during the day, ferrets would generally crouch. They would permit a person on foot to come within 40 feet and a person in a car to come even closer before they would retreat down their burrows. Often they would reappear with only their head showing when the observer was 10 or less feet away and would bob up and down in the burrow entrance. At night, ferrets often could be approached to within a few feet. This was particularly true if use was made of a white light which seemed to partially blind the animals. Females while caring for young were less wary than their offspring or ferrets at other times of the year. The only problem in observation was the initial sighting of a ferret. The animals are quite irregular in visits above ground except for the period from first appearance of the young out of their burrow to family dispersal.

When alarmed or disturbed the ferret gives a characteristic chattering or bark and may hiss defiantly. The animal studied by D. R. Progulske (**unpubl. MS.**) was noted by its original captor to have emitted a squealing note when first run down and seized. At times, a ferret may seemingly challenge a human observer but was never seen to actually attack. Dartt (1879), Aldous (1940), Van Riper and Niedrach (1946), W. E. Garst (**pers. com.**) and D. R. Progulske (**unpubl. MS.**), who have studied either wild or captive individuals, have recorded similar findings on the vocalization and temperament of ferrets. On the basis of certain of the published statements of these authors and of Roosevelt (1900) and Seton (1929), some later writers who have never observed a ferret have pictured it as constantly ferocious and irritable. We believe this is an incorrect judgment. Apparently much of the legend on the disposition of the ferret has come from captive individuals which displayed their anger when provoked or from animals in the wild that were harassed or were defending their young. Actually, Dartt's and Aldous's wild-caught specimens readily submitted to handling and became quite tame. However, Aldous's animal later became wilder when given more freedom.

Ferrets do suffer losses from man. Trapping for various purposes accounts for a few accidentally taken animals. Because of the lack of an assured sizeable catch, however, no commercial market has ever been developed for them. In Europe, though, upwards of 100,000 skins of the European ferret were marketed annually as fitch prior to the 1940's (Harding 1943).

Vehicular traffic is responsible for some loss of ferrets each year. Among the 225 reports of ferrets seen dead or alive, 20 are of ferrets almost certainly run over and killed by motor vehicles on roads. Undoubtedly, many more ferrets have been killed in this manner, and the deaths have been unreported.

Man when he shoots prairie dogs is also a threat to the black-footed ferret. Prairie dog shooting is a popular sport in many places. Some hunters pride themselves on their ability to hit a prairie dog at 200 yards. At such a distance, regardless of the hunter's visual acuity, a ferret peering out of a burrow would be difficult to identify. Some hunters report having killed a ferret because the animal "looked different" and they wanted a closer inspection. Many ferret shootings probably have not been reported because a deliberate killing is a violation of South

Dakota law. Even if the shooting had been accidental, the injured or dead ferret would often disappear down the burrow, leaving no sign of its presence. Lantz (1905) points out that many sport hunters in Kansas persistently killed ferrets whenever they saw one.

Man's greatest threat to the ferret, however, is an indirect one resulting from his destruction of prairie dogs on which ferrets depend for food and shelter. This may have started with reduction by commercial hunters of the bison herds, which through their grazing and trampling activities provided conditions favorable to prairie dogs. However, introduction of domestic livestock probably has compensated at least in part for this influence. More recently man has poisoned prairie dogs or has destroyed their habitat by tillage and other land-use practices.

Prairie dog poisoning has been accomplished with a variety of chemicals but the most effective are strychnine and 1080. They are applied to oats or other grains and distributed at the rate of about 0.04 ounce of actual strychnine (U. S. Dept. Int. 1956) and 0.01 ounce of actual 1080 (C. E. Faulkner **pers. com.**) per acre. The minimum lethal oral dose of 1080 to domestic European fitch ferrets (Marshall 1963) is 1 mg/kg. The level that kills all black-tailed prairie dogs is less than 0.9 mg/kg (Ward and Spencer 1947). We found no data on the toxicity of strychnine to prairie dogs and ferrets. However, lethal oral doses for dogs and cats vary from 0.3 to 1.2 mg/kg, and median lethal oral doses for white rats vary from 5 to 16.2 mg/kg (Spector 1956). Hillman (1968) showed that domestic fitch ferrets died following several feedings on the viscera of prairie dogs killed by eating 1080-poisoned oats. Prairie dogs ordinarily would acquire more than a lethal dose in their feeding on poisoned oats. Hence, a ferret might be poisoned by eating less than all of the parts of a prairie dog containing the poison.

Another probable enemy of the ferret is the badger. On the night of July 9, 1965, a badger entered a part of a prairie dog town where young ferrets were outside their burrow. The mother ferret made a barking sound closely resembling that of a prairie dog. This attracted the badger's attention as it dug into the burrow where the young ferrets had retreated. The badger turned to chase the mother ferret, which disappeared down a burrow located 120 feet from the burrow of the young. The badger then began to dig into the burrow down which the adult ferret had fled. Adrian approached to within a few inches of the badger and took photographs, after which it left the town. It is not known if this burrow had another opening that the ferret could have used as an emergency exit. W. E. Garst (**pers. com.**) recorded an instance in which a badger plugged the entrance of a burrow in which a ferret was heard. The next day the burrow had been dug open from the inside.

The domestic dog definitely seems to be an enemy of the ferret. Three reports of ferrets having been caught and killed by dogs were received from widely scattered localities during an 8-month period: an adult female killed by a dog in Haakon County on September 29, 1965; an adult male killed by dogs in Todd County on March 7 or 8, 1966; and a ferret killed by a dog near a prairie dog town in Jones County in May 1966.

The coyote is also a probable enemy of the ferret. Remains of ferrets were found in 3 of 8,339 coyotes taken with food in their stomachs in western states (Sperry 1941). Some of these coyotes were taken in areas where ferrets were not known to occur. Coyotes commonly hunt prairie dog towns and thus would be apt to encounter ferrets at times.

Two young ferrets were killed by a domestic cat (Cahalane 1954, Report No. 22). Bobcats were noted on prairie dog towns on four different occasions during this study.

Attempted predation by a great horned owl was described in the section on "Senses." In addition, Dale Richardson told us he saw a ferret that was being chased by an owl, run in front of his automobile in Jones County at approximately 3 a.m. on May 16, 1967.

Ralph Hubbard (**pers. com.**) found the dried and badly mutilated remains of a ferret in a golden eagle's nest in the fall of 1912 near Harlowton, Montana. Eagles had used the nest in the spring.

Other potential avian predators of the ferret include the snowy owl and various hawks. On November 11, 1964, at 11:30 a.m., Adrian noted that a ferret which had emerged from a burrow suddenly stopped. At that time a rough-legged hawk lit in the prairie dog town. The prairie dogs began barking an alarm, and the ferret went down a burrow. A ferret sunning itself with its eyes closed would appear to be in danger of predation by raptors. However, this incident indicates that ferrets probably rely on their hearing and the reaction of prairie dogs to warn them of avian hunters.

Prairie rattlesnakes and bull snakes may prey on ferrets at times, but no incidents have been reported.

The young and the adult ferrets in the "south" town in Mellette County seemed to be bothered by external parasites and frequently scratched themselves. Flies, ticks and prairie dog fleas were normally abundant in and around prairie dog burrows used by ferrets. Four ticks on the neck of an adult ferret are shown in Figure

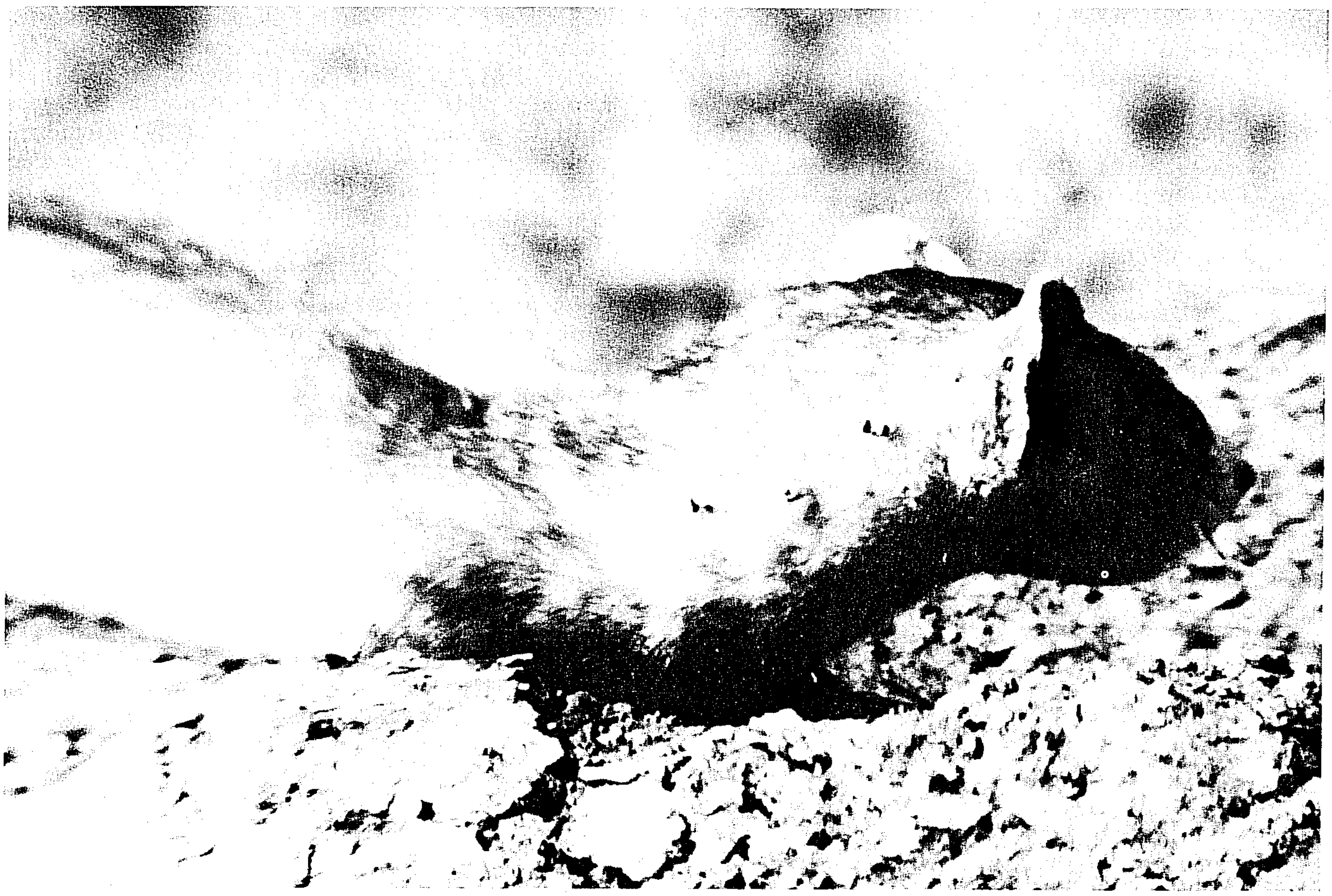

Figure 30. Ticks on neck of adult female black-footed ferret. Mellette County, South Dakota, July 29, 1966. (Henderson)

30. Boddicker (1968) identified the prairie dog flea, a tick **(Ixodes kingi)** and a nematode **(Molineus mustelae)** from three ferrets but found no parasites from four specimens. He also recovered two species of non-parasitic mites. Emerson (1964) lists the louse **(Neotrichodectes minutus)** as a parasite of the ferret.

Little is known about the diseases of black-footed ferrets. The ferret studied by D. R. Progulske **(unpubl. MS.)** was captured in August 1961 as a young animal and held at a mink ranch and later in an outdoor pen containing 12-15 inches of soil and a den box. It died of pneumonia on February 2, 1964. Gorham et al. (1965) describe the diseases and parasites of mink, and Harding (1943) some of those of the domestic European fitch ferret. The longest recorded life span of a black-footed ferret is 5 years for a captive individual (Mann 1930).

LOCATING FERRETS

Solicitation of ferret reports is one of the most efficient means of obtaining potential information on the species within a given area. This may be accomplished by the use of pictures sent to residents in possible ferret areas and published in newspapers and state conservation magazines. For best results it should be accompanied by a brief explanation of the objectives of the survey and of the animal's habits. The color postcards used in this investigation were very effective in prompting the submission of reports.

Since prairie dog towns are the usual residence of the black-footed ferret, the use of a light plane flying at an altitude of 300 to 500 feet is helpful in locating active towns and plotting them on a map. This search may be conducted at any time of the year. However, prairie dog towns are most readily located in the early spring because they "green up" earlier than the surrounding grassland.

Winter is one of the best times for observing signs of ferret activity in prairie dog towns since ferret tracks and digging are most evident in fresh snow. Furthermore, prairie dogs are less active in the winter and not as apt to erase signs of ferret digging. However, snowfalls occur irregularly in western South Dakota. Furthermore, winds easily blow the open prairie land clear of snow or pack the snow so that tracks are not easily visible. Because of its maneuverability a helicopter is probably the most expedient means of surveying a large number of prairie dog towns. However, the operating costs of such equipment are normally high. Therefore, an airplane equipped with skis might be substituted. By flying at elevations of 100 to 200 feet over possible ferret sites, the investigator might easily spot ferret tracks and trenches in fresh snow. Upon sighting possible ferret sign the observer might safely land an airplane in the super-cub class near almost any prairie dog town in South Dakota for a closer inspection from the ground.

In conducting ground surveys of towns during daylight hours the following procedures have been most successful. Approaching to within 100 yards of the area, the investigator should inspect the town through a spotting scope, preferably 15x, or binoculars. It is especially important to note the activity of prairie dogs if any are out. If a ferret is looking out of a burrow or has recently descended a burrow, prairie dogs will not graze peacefully in their normal fashion. Instead, they will usually sit up erectly at their burrow entrance looking in the ferret's direction. They become especially excited and move toward the ferret if it is active above ground. If the ferret goes down a burrow, they will attempt to cover it. It is best to make these initial surveys from a vehicle. Prairie dogs are less wary of the investigator under this condition than if he is on foot.

If observation of prairie dog behavior for 30 minutes yields no indication of a ferret the investigator might profitably proceed as follows: move to the edge of the town and inspect again for 15 to 20 minutes; then, walk or drive around and through the town, looking for ferrets and their sign. The observer should stop occasionally to inspect the area through binoculars. During this survey he may estimate the size of the town.

If this ground search is being conducted in winter, one should look for ferret tracks in the snow or for signs of the playful behavior previously described (snowslides and tunnels, in particular). Burrow openings should be scanned for signs of recent ferret diggings and trench formations. Although ferret scats are rarely found, this sign should not be forgotten.

In addition to signs of digging and trenching, an investigator in summer should note if the town has many freshly covered burrow entrances. Prarie dogs, while usually less active during the winter, will spend many daylight hours at other times of the year plugging burrows in areas where ferrets have been active. During the late spring and early summer the investigator should also notice if the prairie dog population includes as many young prairie dogs as would be expected in a ferret-free prairie dog town. It has been observed that prairie dogs residing in a part of a town occupied by ferrets are more nervous and apt to descend their burrows more readily than those in ferret-free towns. However, this is also true of prairie dogs that have been shot at by hunters.

Nighttime surveys should also be made since the ferret is primarily nocturnal. Mother and young are seen above ground most nights from early July to early September. The principal hours of activity are from the period after twilight to midnight and from 4 a.m. to an hour or so after sunrise (Hillman 1968). A spotlight equipped with a 100-watt aircraft landing bulb is useful in night surveillance. It is best to shine the light back and forth over the same area. A ferret sometimes turns its head away from the light and may not be otherwise discernible except at close distances. The reflection of an artificial white light from a ferret's eyes is brilliant to moderate green and may be detected at distances up to 200 yards. The reflection from a white-tailed jackrabbit or cottontail is amber while that from a badger is light green.

A ferret is usually disturbed by a bright white light. A red filter placed over the light after a ferret is located reduces this annoyance. Also, positioning one's self downwind from the area of observation ensures more normal ferret behavior. Use of an Army infrared snooperscope is not satisfactory for observing ferrets at night. Improved infrared detectors now developed by the Army probably would be more satisfactory. However, this equipment has not been released for civilian use.

Sometimes it is possible to call a ferret out of a burrow by imitating the distress call of a rabbit or prairie dog or the note the mother uses for the young to follow her. This is especially useful if a ferret is known or suspected to be in a particular burrow.

In our opinion, unless ferrets are actually seen, there is no way to be certain that a ferret is living in a prairie dog town at a particular time. Finding any sign characteristic of ferrets should encourage the investigator, but he should keep in mind the similarity of mink sign. The following additional information which can be gathered from nearby residents may also prove helpful in determining the status of ferrets in a prairie dog town: (1) how long has the town been at its present location, (2) is it increasing or decreasing in size, (3) do people shoot at the prairie dogs often, (4) has any poisoning of prairie dogs been attempted, and (5) has anyone seen a ferret or its sign in the town? If the investigator finds sign or if other evidence indicates that further surveillance is warranted, we suggest that the investigator watch and search the town up to 5 consecutive days and nights from 3 hours before dusk until 3 hours after dawn. A two-man team permits observers to alternate.

Towns uninhabited by prairie dogs probably will not yield a ferret. However, they sometimes may be profitably investigated for remaining indications of former ferret presence.

DISCUSSION AND CONCLUSIONS

Black-footed ferrets reportedly have been rare since the species was discovered. This has been due in part to their predominantly subterranean and nocturnal habits accompanied by a lack of concerted effort to find animals and an inability to recognize ferret sign. Surprisingly, however, we uncovered considerably more South Dakota records made during the period preceding the initiation of this study than were generally known to exist. As a result of our investigations, an increased knowledge of ferret habits and sign was obtained. This coupled with greater publicity given to ferret reporting, particularly among ranchers, resulted in many new valid records, in the 4 years from 1964-1968. Obviously ferrets are not as rare in South Dakota as was formerly thought. However, all indications are that they never have been a common species.

Some ferrets persist for a time in situations, such as haystacks, in which prairie dogs are absent. There is no evidence, however, that ferret occupancy separate from prairie dog areas in South Dakota is either extensive or increasing. Whether disappearance of ferrets from such areas is the result of an uncertain food supply, lack of ready-made burrows, or innate behavior patterns is unknown.

Based on present animal control attitudes and philosophies the outlook for the prairie dog on private land is not bright. Some private landowners tolerate small numbers of prairie dogs, and a few commercial establishments feature prairie dog towns as tourist attractions. However, many landowners desire eradication of the prairie dog and either do it themselves or ask for government assistance. In addition, pressures exist for governmental control of prairie dogs on many Indian reservations and on certain public lands.

Before man undertakes any large-scale intensive program for control of any organism, he should know the impact of that program on other organisms. If dangers exist, adequate steps should be taken to keep them at a tolerable level. Removal of any native species might have far-reaching effects on the other members of the ecological community since each is related to the rest. We still have much to learn about the prairie dog and its relationship to the rest of the prairie community. We know even less about the black-footed ferret. However, all information available to us indicates a close association of the two species in South Dakota and perhaps even a necessary dependency of the ferret upon the prairie dog if the ferret is to exist in any numbers. Therefore, we conclude that a program for preservation of ferrets becomes, as well, a program for retention of adequate numbers of prairie dogs.

In order to preserve the ferret, we recommend the following over-all program:

1. Continue and intensify studies into the status, life history and ecological relationships of ferrets, prairie dogs, and other ferret prey. This should include development of methods to live-trap and mark ferrets and investigations of marked ferrets to learn their movements and longevity.
2. Continue efforts to develop better methods for determining the presence of ferrets.
3. Urge increased reporting by the public of live and dead ferrets and of ferret sign. Reports should be sent to the South Dakota Department of Game, Fish and Parks at Pierre 57501 or to the Bureau of Sport Fisheries and Wildlife, Ferret Biologist, 919 Main, Rapid City, South Dakota 57702, or given to employees of the Department or Bureau.
4. Promote greater public awareness of the dependency of ferrets upon prairie dogs.
5. Determine the direct and indirect effect of prairie dog control on ferrets.
6. Develop materials for prairie dog and other animal control that will not poison ferrets.
7. Explore all feasible means of retaining adequate numbers of prairie dogs and ferrets on both public and private lands.
8. Experiment with transplanting and releasing ferrets into areas where prairie dogs are protected.
9. Test methods for maintaining ferrets in areas not occupied by prairie dogs.
10. Employ a state wildlife biologist to study non-game animals, including ferrets.

The black-footed ferret is protected in South Dakota. No one except authorized personnel may hunt, take, trap or kill a ferret, and then only under severe restrictions. In regard to prairie dogs, no control may be undertaken on national wildlife refuges of the U. S. Bureau of Sport Fisheries and Wildlife without permission of the Regional Director of that region. Further policy issued June 22, 1965, states that U. S. Department of the Interior personnel may not undertake prairie dog control until surveys are conducted and the areas are certified to be free of ferrets. The U. S. Department of Agriculture and the Defense Department are also cooperating by generally requiring pre-control surveys on lands under their jurisdiction.

The present method of pre-treatment survey is by vehicle or on foot. Our studies have shown that the occurrence of ferrets or their sign varies considerably. Even the most qualified observer cannot make a survey of a prairie dog town in a limited time and always say with full assurance that ferrets are not present. We watched two different towns for a 5-day period and saw ferrets on several nights. However, these ferrets left no visible sign during this time. To be sure that a ferret does not occupy a prairie dog town, we believe a survey crew should plan on spending up to 5 consecutive days and nights observing the town.

Necessary control rather than eradication of prairie dogs is the current objective of the Bureau of Sport Fisheries and Wildlife. Also, under a new experimental policy announced April 27, 1967, the Bureau will not attempt to achieve complete prairie dog control by follow-up poisoning if the first treatment achieves approximately 90 per cent control.

We have found that landowners who wish to control prairie dogs in towns on their property that are harboring one or more ferrets are sometimes satisfied to forego poisoning when it is explained to them that ferrets eat prairie dogs and are able to stabilize or reduce prairie dog populations.

If land where prairie dog control is desired is leased from a government agency for grazing, it may be possible to lower the cost of the lease to a level commensurate with the current value of the land for cattle. This would tend to reduce the pressure for increased prairie dog control on land that is overevaluated.

In key private areas another approach might be to lease the rights from the landowner not to poison the town. This would be similar to governmental programs of leasing the rights not to drain, fill or burn wetlands. At present, governmental agencies do not have funds set up specifically for a lease program of non-poisoning. However, such an approach is possible under the federal Rare and Endangered Species Program. In addition, some private conservation organizations might have limited funds that could be used to lease non-poisoning rights in important areas.

If prairie dog poisoning is undertaken, treating only the perimeters of towns to prevent their further increase in size is preferable to complete poisoning.

Accurate information on the home range of ferrets still does not exist. However, we believe restricting placement of poison for control of prairie dogs and other animals within a 5-mile radius of any known ferret location should give adequate protection to ferrets.

More study is needed of the secondary effects of present prairie dog poisoning programs on ferrets. In addition, increased steps should be taken to develop materials that do not jeopardize non-target species. In this regard the report of the Secretary of the Interior's Advisory Board on Wildlife Management (Leopold 1964) recommended that legal means be explored to ban the distribution and use of 1080 as a poison for field rodents and that such control be conducted with other chemicals which are not readily transmitted to scavenging animals.[1]

One way of providing prairie dog towns for ferrets is on governmental parks and refuges. In South Dakota some of these areas are Custer State Park, Badlands National Monument, Wind Cave National Park, Lacreek National Wildlife Refuge, several National Grasslands and National Forests administered by the U. S. Forest Service, lands under the trusteeship of the Bureau of Indian Affairs, and lands administered by the Bureau of Land Management. An attempt should be made at an early date to inventory and estimate the numbers of ferrets and prairie dogs now present on these areas. If ferrets are found near these lands, the possibility of public acquisition should be ascertained. At times some governmental lands are determined to be in excess to the public need. It is recommended that they not be transferred to private interests if they have ferrets or conditions suitable for the establishment of prairie dog towns in which ferrets could reside.

No ferrets are now known to exist in Custer State Park, Badlands National Monument or Wind Cave National Park. Since these areas have protected prairie dog towns, it is recommended that they be stocked with ferrets at some future time if surplus animals can be found in other areas. Such animals should be marked to provide information on their movement and longevity.

The Bureau of Sport Fisheries and Wildlife under the Rare and Endangered Species Program has a biologist who, since February 1966, has been assigned full time to studies on ferret. These include investigations of status and movements of ferrets, improved survey methods, and determination of effects of prairie dog control programs on ferrets. However, more effort is needed. In addition the state of South Dakota has increasing interest in pest animal control. For these reasons the employment of a state biologist to work on ferrets and other non-game species is recommended to develop pest control programs.

For over a century the black-footed ferret has remained shrouded in mystery. As a result of this study we have gained new insight into the habits of this animal and its relationship to various facets of its environment including the prairie dog control program. Although additional knowledge is needed on some points, we presently possess much of the basic information necessary to manage this species for the future. The moral responsibility of all men to see that the black-footed ferret is allowed to remain a part of our original prairie heritage is now at hand.

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1. The Bureau of Sport Fisheries and Wildlife no longer uses 1080 for prairie dog control.

References Cited

Aldous, Shaler E. 1940. Notes on a black-footed ferret raised in captivity. J. Mammal. 21(1):23-26.

Allen, Glover M. 1942. Extinct and vanishing mammals of the western hemisphere. Am. Com. Internatl. Wild Life Protection Spec. Publ. 11. 620 p.

Anonymous. 1889. The black-footed ferret. Forest and Stream 32(17):335.

__________. 1906. Black-footed ferrets. Trappers World. 4(2):20.

Anthony, H. E. (Editor). 1937. Mammals of America. Garden City Publ. Co., N. Y. 335 p.

Audubon, John James, and John Bachman. 1851. The viviparous quadrupeds of North America. Vol. II. V. G. Audubon, N. Y. 334 p.

Bailey, Vernon. 1926. A biological survey of North Dakota. U. S. Dept. Agr. N. Am. Fauna No. 49. 226 p.

Baker, A. B. 1889. Mammals of western Kansas. Trans. 20th and 21st Annual Meeting Kans. Acad. Sci. 11:56-58.

Bissonnette, T. H. 1938. Experimental control of sexual photoperiodicity in animals and possible applications to wild life management. J. Wildl. Mgmt. 2 (3) :104-118.

Boddicker, M. L. 1968. Parasites of the black-footed ferret. Proc. S. D. Acad. Sci. 47: 141-148.

Brons, H. A. 1882. Notes on the habits of some western snakes. Am. Naturalist 16(7):564-567.

Burnett, W. L. 1915. The prairie-dog situation in Colorado. Office Colo. State Entomol. Circ. 17. 15 p.

Burt, William H., and Richard P. Grossenheider. 1964. A field guide to the mammals. Houghton Mifflin Co., Boston. 284 p.

Cahalane, Victor H. 1954. Status of the black-footed ferret. J. Mammal. 35(3):418-424.

Cottam, Clarence, and Milton Caroline. 1965. The black-tailed prairie dog in Texas. Texas J. Sci. 17(3):294-302.

Coues, Elliott. 1877. Fur-bearing animals — a monograph of the North American Mustelidae. Dept. Interior U. S. Geol. Survey of the Territories Misc. Publ. No. 8. 348 p.

Crandall, Lee S. 1964. The management of wild mammals in captivity. Univ. Chicago Press. 769 p.

Dartt, Mary. 1879. On the plains and among the peaks. Claxton, Remsen and Haffelfinger, Phila. 237 p.

Elder, William H. 1951. The baculum as an age criterion in mink. J. Mammal. 32(1):43-50.

Emerson, K. C. 1964. Checklist of the Mallophaga of North America (north of Mexico). Pt. I. Suborder Ischnocera. Dugway Proving Ground, Dugway, Utah. 171 p.

Garst, W. E. 1954. Black-footed ferret in South Dakota. J. Mammal. 35(4):594.

Gorham, J. R., H. J. Griffiths, and R. Keith Farrell. 1965. Minks: diseases and parasites. U. S. Dept. Agr. Handbook No. 175. 38 p.

Grinnell, George Bird. 1895. The story of the Indian. D. Appleton Co., N. Y. 270 p.

__________. 1896. Range of the black-footed ferret. Forest and Stream 47(5):84.

Hall, E. Raymond. 1955. Handbook of mammals of Kansas. Univ. Kans. Museum Nat. Hist. Misc. Publ. 7. 303 p.

__________, and Keith R. Kelson. 1959. The mammals of North America. Vol. II. Ronald Press Co., N. Y. 617 p.

Harding, A. R. 1943. Ferret facts and fancies. A. R. Harding Pub. Co., Columbus, Ohio. 214 p.

Hillman, Conrad N. 1968. Field observations of black-footed ferrets in South Dakota. Trans. N. Am. Wildl. and Nat. Resources Conf. 33: 133-143.

Hoffmeister, Donald F. 1963. Mammals. Golden Press, N. Y. 104 p.

Homolka, Charles L. 1964. Our rarest mammal? Audubon Mag. 66(4):244-246.

Kellogg, A. Remington. 1960. Mammals and how they live. P. 13-35. In Wild mammals of North America. Natl. Geog. Soc., Washington, D. C. 400 p.

Koford, Carl B. 1958. Prairie dogs, whitefaces, and blue grama. Wildl. Monographs No. 3. 78 p.

Lantz, D. E. 1905. Kansas mammals in their relations to agriculture. Kans. State Agr. Coll. Expt. Sta. Bull. No. 129, p. 331-404.

Leopold, A. S. (Chairman). 1964. Predator and rodent control in the United States. Trans. N. Amer. Wildl. and Nat. Resources Conf. 29:27-47.

Longhurst, William. 1944. Observations on the ecology of the Gunnison prairie dog in Colorado. J. Mammal. 25(1):24-36.

Mann, William M. 1930. Wild animals in and out of the zoo. Smithsonian Sci. Ser. Vol. 6. 362 p.

Marshall, William H. 1935. Mink displays sliding habits. J. Mammal. 16(3):228-229.

__________. 1963. The ecology of mustelids in New Zealand. N. Z. Dept. Sci. Indus. Research Infor. Ser. No. 38. 32 p.

McCandless, A. D. 1908. A week in the saddle. Forest and Stream 71(9)329-330.

Mead, J. R. 1885. Notes of two Kansas mammals. Bull. Washburn Coll. Lab. Nat. Hist. 1(3):91-92.

Moon, G. F. 1905. What have I got? Trappers World. 1(5):4.

Murie, Olaus J. 1954. A field guide to animal tracks. Houghton Mifflin Co., Boston. 374 p.

Nelson, Edward W. 1918. Smaller mammals of North America. Natl. Geog. Mag. 33(5):371-493.

Olin, George. 1959. Mammals of the southwest deserts. Second ed., revised. Southwestern Monuments Assoc. Popular Ser. No. 8. 112 p.

Peterson, Liven A., and Elihu D. Berg. 1954. Black-footed ferrets used as ceremonial objects by Montana Indians. J. Mammal. 35(4):593-594.

Presnall, Clifford C. 1963. Inventory of areas occupied by prairie dogs — 1961. U. S. Fish and Wildl. Serv. Branch of Predator and Rodent Control Circ. Letter May 10, 1963. 3 p.

Reagen, Albert B. 1908. Notes on the flora and fauna of the Rosebud Reservation, west of Gregory County. P. 143-167. In Report of State Geologist, S. D. Geol. Survey Bull. No. 4. 229 p.

Roosevelt, Theodore. 1900. The wilderness hunter. G. P. Putnam's Sons, N. Y. 472 p.

Seton, Ernest Thompson. 1929. Lives of game animals. Vol. II, Pt. II, p. 565-574, 579-632 and Vol. IV, Pt. I, p. 275-298. Doubleday, Doran Co., Garden City, N. Y.

Smith, Ronald E. 1967. Natural history of the prairie dog in Kansas. Univ. Kans. Museum Nat. Hist. and State Biol. Survey Misc. Publ. 49. 39 p.

Spector, William S. (Editor). 1956. Handbook of toxicology. Vol. I. Acute toxicities of solids, liquids and gases to laboratory animals. W. B. Saunders Co., Phila. 408 p.

Sperry, Charles C. 1941. Food habits of the coyote. U. S. Fish and Wildl. Serv. Wildl. Research Bull. 4. 70 p.

Strecker, J. K., Jr. 1910. Notes on the fauna of a portion of the Canyon region of northwestern Texas. Baylor Univ. Bull. 13(4-5):1-31.

U. S. Dept. of Interior. 1956. Prairie dogs and their control. Fish and Wildl. Serv. Wildl. Leaflet 357. 4 p.

__________. 1964. Rare and endangered fish and wildlife of the United States. Compiled by Com. on Rare and Endangered Wildl. Species, Bur. Sport Fisheries and Wildlife: 62 p.

Van Riper, Walker, and Robert J. Niedrach. 1946. Black-footed ferret. Nat. Hist. 55(10):466-467.

Ward, Justus C., and D. A. Spencer. 1947. Notes on the pharmacology of sodium fluoroacetate — compound 1080. J. Am. Pharm. Assoc., Sci. Ed. 36(2):59-62.

Warren, Edward R. 1942. The mammals of Colorado. Univ. Okla. Press, Norman. 330 p.

Westin, Fred C., Leo F. Puhr, and George J. Buntley. 1959. Soils of South Dakota. S. Dak. State Coll. Agr. Expt. Sta. Soil Survey Ser. No. 3. 34 p.

Wilcomb, Maxwell J., Jr. 1954. A study of prairie dog burrow systems and the ecology of their arthropod inhabitants in central Oklahoma. Ph. D. Thesis, Univ. Okla., Norman. 158 p.

Young, Stanley P. 1946. Sketches of American wildlife. Monumental Press, Baltimore. 143 p.

__________. 1954. Black-footed ferret (Mustela nigripes) in South Dakota. J. Mammal. 35(3):443.

Ferret Specimens and Sightings In South Dakota From 1889 To 1967

1889

1. 1889 — skin seen, animal not common — Pine Ridge Agency, Shannon County. Reported by A. B. Baker. Bureau of Sport Fisheries and Wildlife records.

1894

2. 1894 — reported to be plentiful — Sand Ridge, north of Cheyenne River, between its mouth and the fork, Dewey and Ziebach Counties. Recorded by Vernon Bailey. Bureau of Sport Fisheries and Wildlife records.

1903

3. 1903 or 1904 — one — Gillette Canyon, Custer County. Observed in prairie dog town by James P. Campbell. Recorded by Merritt Cary. Bureau of Sport Fisheries and Wildlife records.

1904

4. 1904 — one — Indian Draw near Sheep Mountain, Pennington County. Observed by Abraham Jefferson. Recorded by Merritt Cary. Bureau of Sport Fisheries and Wildlife records.

1905

5. About 1905 — two — Okobojo, Sully County. Pair came in and cleaned out prairie dog town. Reported by J. W. Glessner. Recorded by Merritt Cary. Bureau of Sport Fisheries and Wildlife records.
6. Spring — four — Bailey (S 26, T 109 N, R 70 W), Hand County. Trapped by G. F. Moon. Pair sold alive and two mounted (Moon 1905 and Anon. 1906).
7. Winter — 1905-1906 — one — southern Bennett County just across state line from Merriman, Nebraska. Killed and mounted by L. Sessions. Bureau of Sport Fisheries and Wildlife records.

1907

8. About 1907 — more than one — Rosebud Indian Reservation; Mellette, Todd and Tripp Counties (Reagen 1908).

1908

9. 1908 — unspecified number — Okobojo Creek, Sully County. Ferrets destroyed prairie dogs in immense town. Reported by S. W. Glenn. Bureau of Sport Fisheries and Wildlife records.

1913

10. January 10 — one — Box Elder, Pennington County. Collector unknown. Specimen J 23 mounted, W. H. Over Dakota Museum, University of S. D. Recorded by Byron E. Harrell.

1915

11. August 22 — male — labelled Pine Ridge (Indian) Reservation, White River, Mellette County. Collected by R. A. Ward. Specimen 209150, U. S. National Museum. Recorded by Paul F. Springer.
12. October — one — Badlands, Pine Ridge Indian Reservation, northern Shannon County. Observed by H. H. Sheldon. Bureau of Sport Fisheries and Wildlife records.

1920

13. October 4 — male — Interior, Jackson County. Trapped in prairie dog town by Bud Dalrymple. Bureau of Sport Fisheries and Wildlife records.

1921

14. February 11 — male — along Cheyenne River near Scenic, Pennington County. Trapped in prairie dog town by Bud Dalrymple. Bureau of Sport Fisheries and Wildlife records.

1922

15. Spring — one — Wind Cave National Park, Custer County. Observed in prairie dog town by Troy C. Beach. (Hot Springs (S. D.) Times Herald; April 21, 1922.)

1923

16. 1923 — one — along Eagle Nest Creek, Washabaugh County. Trapped in prairie dog town by Vetal Romero. Recorded by F. Robert Henderson.
17. September 16 — one (sex not stated) — Pine Ridge, Shannon County. Collected by D. P. Stearns. Specimen 243799, U. S. National Museum. Recorded by Paul F. Springer.
18. November 1— male — Govert, (S15, T15N, R8E), Harding County — collected by Louis Knowles. Specimen 243990, U. S. National Museum. Recorded by Paul F. Springer.

1925

19. Before November 5 — female — Pine Ridge, Shannon County. Specimen 241014, U. S. National Museum. Recorded by Paul F. Springer.
20. December 24 — male — T 2 S, R 12 E, Pennington County. Trapped by Mr. Rockwell. Submitted by Ray E. Lemley. Specimen 70590, American Museum of Natural History. Recorded by Richard G. Van Gelder.

1927

21. September 5 — female — 18 miles southeast of Rapid City, Pennington County. Collected in prairie dog town along Spring Creek by Henry Behrens, Sr. Specimen mounted, Augustana College, Sioux Falls. Recorded by Paul F. Springer.
22. Winter — one — near Conata, Pennington County. Collected in prairie dog town by Thad Bennett. Specimen J155, Zoology Department, University of S. D. Recorded by Byron E. Harrell.

1930's

23. 1930's — several — northeast of Lantry along Moreau River, Dewey County. Observed in prairie dog town by Wesley E. Ernst. Recorded by Fred Priewert.
24. 1930's — one — 17 miles northeast of White River, Mellette County. Observed in prairie dog town by Albert Jans. Recorded by Paul F. Springer and Conrad Hillman.

1931

25. Spring — several — Crow Creek Indian Reservation, probably Buffalo County. Observed by Tom J. Turner.
26. December 31 — male — near Hermosa, Custer County. Trapped in prairie dog town by Fred M. Dille. Specimen ZM 4451, University of Nebraska Museum. Recorded by Paul F. Springer.

1937

27. 1937 — one — T 4 N, R 15 E, Pennington County. Observed in prairie dog town by Evan McDonald. Recorded by F. Robert Henderson.

1940

28. Fall — one — T 16 N, R 15 E, Perkins County. Found dead on road in prairie dog town by Earl Engelbretson. Recorded by Paul F. Springer.

1946

29. 1946 or 1947 — male — T 19 N, R 23 E, Corson County. Trapped by John Steel. Recorded by Paul F. Springer.
30. November — male — Lyman County. Collected in prairie dog town by Adrian Lester. Specimen 33434, State University of Iowa. Recorded by Walter C. Thietje.

1947

31. About July 15 — one — T 2 S, R 22 E, Jackson County. Ferret picked up a shot prairie dog and took it down a burrow. Observed by A. Orville Sandall.

1948

32. Spring — one — near Chamberlain, Brule County. Recorded by James T. McBroom. (Cahalane 1954, Report No. 30).

1949

33. About 1949 — one — near Mud Butte, Meade County. Observed by Clarence Allen. Recorded by Douglas R. West.

1950

34. Summer — six — north of Parmelee, Rosebud Indian Reservation, Todd and Mellette Counties. Observed in prairie dog towns by Walter J. Stammerjohn. Recorded by Harold H. Haecker. (Cahalane 1954, Report No. 23).
35. Summer — one — on Baxter Berry ranch between Norris and Belvidere, Mellette County. Observed in prairie dog town by Ralph Block.
36. Summer — one — fork of White River, northeast of Blackpipe Day School, Mellette County. Observed in prairie dog town by Ralph Block.
37. October — two — 12 miles south of Isabel, Dewey County. Observed in prairie dog town by Ralph Block; one male shot. Specimen 285877, U. S. National Museum. Recorded by Paul F. Springer. (Cahalane 1954, Report No. 25 corrected).

1951

38. 1951 or 1952 — one — T 114 N, R 79 W, Sully County. Observed along creek by E. R. Lamster.
39. 1951 or 1952 — one — Wessington Springs, Jerauld County. Trapped by unknown person. Reported by Robert N. Randall. Recorded by John L. Sypulski. (Cahalane 1954, Report No. 32).
40. Summer — at least two — north of Rosebud Indian Agency, Mellette County. Observed in prairie dog town by Harvey Gibson. Recorded by Harold H. Haecker. (Cahalane 1954, Report No. 26).
41. Summer — one — northwest of Oglala, Pine Ridge Indian Reservation, Shannon County. Observed in prairie dog town by Ralph Block. (Cahalane 1954, Report No. 24 corrected).
42. Summer — one — near Kyle, Pine Ridge Indian Reservation, Shannon County. Observed in prairie dog town by Ralph Block. (Cahalane 1954, Report No. 24 corrected).
43. Fall — one — near Mobridge, Walworth County. Trapped by unknown person. Recorded by James T. McBroom. (Cahalane 1954, Report No. 31).
44. November — one — Okobojo Creek, Sully County. Shot by unknown person. Reported by John W. Leete. Recorded by John L. Sypulski. (Cahalane 1954. Report No. 33).

1952

45. Summer — two — north of Cheyenne River, Meade County. Trapped in prairie dog town by unknown person. Reported by Roy L. Clennon. Recorded by Oren Bates. (Cahalane 1954, Report No. 34).
46. Summer — four young — south of Lemmon, Perkins County. Observed in nest in haystack by unknown person. Reported by W. L. Johns. Recorded by Harold H. Haecker. (Cahalane 1954, Report No. 29).
47. Summer — six — eastern Pennington County including two in Conata Basin, T 3 S, R 16 E. Observed in prairie dog town by George Barnes. Recorded by Harold H. Haecker. (Cahalane 1954, Report No. 28). Female specimen 287321, U. S. National Museum, from Conata Basin is probably one of these animals.
48. Summer — six — on Pine Ridge and Rosebud Indian Reservations, Shannon, Washabaugh, Todd and Mellette Counties. Observed by Harvey Gibson. Recorded by Harold H. Haecker. (Cahalane 1954, Report No. 27).
49. Summer — one — 5 miles northeast of Philip, Haakon County. Observed in prairie dog town by unknown person. Reported by W. H. Zimmerman. Recorded by M. S. McMurtrey. (Cahalane 1954, Report No. 37).
50. October 23 — female — 4 miles north of North Fork of Moreau River near Zeona, Perkins County. Run over on road by brother of Alfred Hinds. (Young 1954). Specimen 3667 mounted, J. F. Bell Museum of Natural History, Mpls. Recorded by Paul F. Springer.

1953

51. Early July — two adults — 11 miles east of Howes, Ziebach County. Observed in prairie dog town by Ralph Block. One young sighted with adults in same place 2 weeks later. (Cahalane 1954, Report No. 35).
52. July — one — along Bull Creek, 2 miles northeast of Howes, Meade County. Observed in prairie dog town by Ralph Block. (Cahalane 1954, Report No. 36).
53. July 30-August 11 — six — T 1 N, R 24 E, Haakon County. Five trapped in prairie dog town by George Barnes; believed to be adult and four young. Two died in captivity but two males and a female were released in Wind Cave National Park, Custer County. One animal shown in film "Vanishing Prairie." (Garst 1954; Cahalane 1954, Report No. 38).
54. September — one — U. S. Highway 14, 1 mile west of Midland, Haakon County. Found dead on road by Ben Buell. Recorded by George Barnes.

1954

55. About 1954 — one — T 10 N, R 15 E, Meade County. Run over and stunned by William Jordan. Put in barn but escaped. Recorded by Douglas R. West.
56. March 24 — male — U. S. Highway 14, 15 miles north of Midland, Stanley County. Found dead on road by Bernard A. Nelson.
57. August — one — 7 miles northeast of Kadoka, Jackson County. Observed in prairie dog town by James Judge. Recorded by Harold H. Haecker.
58. November — male — near Moreau River, 14 miles northwest of Dupree, Ziebach County. Trapped by Robert Burgee.
59. November — male — near Red Elm, Ziebach County. Killed on trail by Robert Burgee.
60. Late fall — female — T 17 N, R 23 E, Dewey County. Shot ½ mile from prairie dog town by Ed Bickel.

1955

61. About 1955 — one — 15 miles south of Kennebec, Lyman County. Found dead on road by Kenneth E. Christensen. Recorded by Walter H. Kittams.
62. About 1955 — one — T 8 N, R 16 E, Meade County. Run over on road by Henry McKay. Recorded by Paul F. Springer.
63. About 1955-1958 — two — 7 miles north of White River, Mellette County. Animals caught in prairie dog town by Charles Larson but escaped. Recorded by William Pullins and Walter H. Kittams.
64. April 13 — one — 16 miles northwest of Jordan Junction, Tripp County. Observed in prairie dog town by John L. Seubert.
65. September — one — T 14 N, R 25 E, Dewey County. Observed in den along Goose Creek by Harold H. Haecker.

1956

66. About 1956 or 1957 — two — 17 miles north of Camp Crook, Harding County. Observed in prairie dog town by Einer Juntti. Recorded by Robert Murphy and Walter H. Kittams.
67. Summer — one — T 22 N, R 29 E, Corson County. Observed in prairie dog town by Ralph Block.
68. Mid summer — one — west edge of Madison, Lake County. Sick ferret found in granary by farmer; died the next day. Skin in Wilbur C. Foss Collection.
69. August 1 — one large and two small ferrets together plus another small ferret nearby — T 20 N, R 28 E, Corson County. Observed in prairie dog town by Walter J. Stammerjohn.
70. Fall — one — Cedar Pass, Badlands National Monument, Jackson County. Observed killing cottontail rabbit near prairie dog town by Tom Boothroyd. Recorded by Walter H. Kittams.
71. Fall 1956 or 1957 — one — about 7 miles west of Gettysburg, Potter County. Reported in prairie dog town by Walter Larsen. Recorded by Walter H. Kittams.

1957

72. About 1957 — one — 7 miles south of White River, Mellette County. Trapped in prairie dog town by Rollie Johnson. Recorded by William Pullins and Walter H. Kittams.
73. About 1957 — one — near Presho, Lyman County. Observed crossing road in evening by Robert Zimbelman. Recorded by Walter H. Kittams.
74. July — one — T 17 N, R 21 E, Ziebach County. Observed by Ed Bickel. Recorded by Paul F. Springer.
75. About August 28 — four (believed to be two adults and two young) — T 41 N, R 33 W, Washabaugh County. Observed in prairie dog town by William Pullins.
76. September — six — about 22 miles west of Onida, Sully County. One shot by landowner in 80-acre prairie dog town. Reported to Ernest Giese.
77. September — one — 8 miles southwest of Agar, Sully County. Observed in a 5-acre prairie dog town by Ernest Giese and Charles Cadieux.

78. September — three — about 18 miles southwest of Onida, Sully County. Observed in 100-acre prairie dog town by unknown person. Recorded by Ernest Giese.

1958

79. About 1958 — one — 12 miles northwest of Highmore, Hyde County. Observed fighting with prairie dog by Joe Stranski. Recorded by Paul F. Springer.
80. About 1958 — one — near Seven Mile Corner, Jackson County. Found dead on road by Jack Hansen. Recorded by F. Robert Henderson.
81. About 1958 or 1959 — one — 27 miles west of Onida, Sully County. Observed in prairie dog town by R. M. Hinsey. Recorded by John Hunter and Walter H. Kittams.
82. January — male — 5 miles southeast of Faith, Ziebach County. Observed in haystack by Dono Capp. Recorded by Douglas R. West. Skin in Douglas R. West Collection.
83. Summer — adult male — U. S. Highway 16, 2 miles west of Reliance, Lyman County. Found dead on road by Robert F. Wahlin.
84. Summer — one — 2 miles east of Sitting Bull Monument, Walworth County. Observed in prairie dog town by Ralph Block. Recorded by Walter H. Kittams.
85. Summer — one — near Midland, Haakon County. Found dead on road by Jack Huston. Recorded by John Hunter and Walter H. Kittams.
86. Fall — one — on Pat Parkening ranch, northwest of Reliance, Lyman County. Observed in prairie dog town by Robert F. Wahlin.
87. Fall — male and female — 20 miles southeast of Faith, Ziebach County. Caught in prairie dog town by Don Thompson. Female released after killing male. Two others caught next spring. Recorded by Walter H. Kittams.
88. September — one — White River, Mellette County. Killed by domestic dog in prairie dog town at edge of city. Observed by Alfred Bartlett. Recorded by William Pullins and Walter H. Kittams.
89. Winter 1958-1959 — one — 15 miles south of Kennebec, Lyman County. Found dead in mink trap by Kenneth E. Christensen. Recorded by Walter H. Kittams.

1959

90. About 1959 — male — 10 miles south of White River, Mellette County. Shot in prairie dog town by Ted Johnson. One of the lower canine teeth had grown out forward from the mouth, but ferret was in good condition. Recorded by F. Robert Henderson and Richard Adrian.
91. Spring — one — near Ideal, Tripp County. Observed in 30-acre prairie dog town by Harold Davis and Lloyd Oldenburg. Recorded by Walter H. Kittams.
92. Summer — one — near Agar, Sully County. Caught in and released from rat trap on turkey farm. Recorded by Walter H. Kittams.
93. Summer — one — T 41 N, R 34 W, Washabaugh County. Observed near prairie dog town by Paul Brunch's son. Recorded by Walter H. Kittams.
94. Summer 1959 or 1960 — four — near Midland, Haakon County. Observed on road at night by Jack Huston. Recorded by John Hunter and Walter H. Kittams.
95. Fall — one — between Longvalley and Norris, Washabaugh County. Observed along road by Paul Brunch. Recorded by Walter H. Kittams.
96. Fall — adult male — 12 miles west of Agar, Sully County. Found dead on road, ¾ mile from 80-acre prairie dog town by Orville VonWald. Recorded by Tal Lockwood. Specimen mounted, S. D. Department of Game, Fish and Parks.
97. Fall 1959 or 1960 — one — near Midland, Haakon County. Observed standing along side of road by Jack Huston. Recorded by John Hunter and Walter H. Kittams.
98. September — one — 2 miles north of Maurine, Perkins County. Found dead on road in prairie dog town by Dale Haines. Recorded by William Pullins and Walter H. Kittams.
99. September 24 — three — along Okobojo Creek about 25 miles southwest of Onida, Hughes County. Observed in 30-acre prairie dog town by Floyd brothers. Recorded by Dean Badger and Walter H. Kittams.

1960

100. About 1960 — one — northeast of Gregory, Gregory County. Killed by domestic dog. Observed by Lloyd Gilbert. Recorded by Richard Adrian.
101. 1960 or 1961 — one — 10 miles south of Highmore, Hyde County. Observed in prairie dog town by Mrs. Joe Stranski. Recorded by Paul F. Springer.
102. Summer — one — on Albert Larson ranch southeast of Reliance, Lyman County. Observed in prairie dog town by Robert F. Wahlin.
103. Summer — one — T 41 N, R 35 W, Washabaugh County. Found dead on road by Wayne Allen. Recorded by Richard Adrian.
104. Late summer — one — 5 miles north of Red Elm, Ziebach County. Observed in 60-acre prairie dog town by Robert Burgee.
105. About August — one — along S. D. Highway 34, 25 miles east of Sturgis, Meade County. Observed crossing road by Wilbur Bachard. Recorded by Douglas R. West.
106. Fall — one — along Cheyenne River southeast of Eagle Butte, Dewey County. Observed in 300-acre prairie dog town by Robert Burgee.
107. October 22 — young male — 9 miles west of Onida, Sully County. Found dead on road, 4 miles from 30- to 40-acre prairie dog town by Dean Badger and Tal Lockwood. Recorded by Walter H. Kittams. Specimen 238132 (mounted), U. S. National Museum.
108. December — one — near Lodgepole, Perkins County. Found dead in trap, 10 miles from prairie dog town, by Woodrow Lewton. Recorded by Douglas R. West and Walter H. Kittams.

1961

109. March 3 — one — Sage Creek Basin, Badlands National Monument, Pennington County. Observed in small prairie dog town by Jack Close. Recorded by Robert Powell and Walter H. Kittams.
110. August — young male — along road 3 miles north of Reliance, Lyman County. Caught at night by Calvin F. Anderson. Kept at mink farm at Mitchell until February 16, 1963. Transferred to S. D. State University. Died February 2, 1964. Mounted specimen, Department of Wildlife Management.

1962

111. About 1961 — one — about 2 miles southwest of Sheep Mountain Table, Shannon County. Observed by C. M. Jurisch. Recorded by Paul F. Springer.
112. 1962 or 1963 — one — 4 miles northeast of Scenic, Pennington County. Observed in prairie dog town by Ralph Burroughs. Recorded by Paul F. Springer.
113. Summer — one — T 42 N, R 36 W, Washabaugh County. Observed catching thirteen-lined ground squirrel in alfalfa field by Loras Riggins. Recorded by Richard Adrian.
114. Summer 1962 or 1963 — one — 2½ miles south of Blunt, Hughes County. Killed in prairie dog town by son of Henry Lauing. Recorded by Donald R. Progulske and Paul F. Springer.
115. About August — one — along U. S. Highway 14, 2 miles east of Highmore, Hyde County. Observed by George M. Jonkel.

1963

116. About 1963 — one — 5 miles northwest of Mound City, Campbell County. Observed in prairie dog town by Orville Kautz. Recorded by F. Robert Henderson.
117. About 1963 — one — T 2 S, R 13 E, Pennington County. Observed by Marlow Jurisch. Recorded by Paul F. Springer.
118. March — one — near Ladner, Harding County. Observed in prairie dog town by Wesley Broer. Recorded by Donald R. Progulske.
119. Summer — one — T 39 N, R 31 W, Todd County. Observed in prairie dog town by Bryan Provancial. Recorded by Richard Adrian.

120. Summer — one — T 39 N, R 31 W, Todd County. Observed in prairie dog town (different from above) by Bryan Provancial. Recorded by Richard Adrian.

121. August 3 — skull — near Hidden Timber, Todd County. Observed in prairie dog town by John Hunter.

122. Summer — one — T 16 N, R 15 E, Perkins County. Observed chasing prairie dog by Raymond Saunders. Recorded by Douglas R. West.

123. August — one — T 40 N, R 30 W, Mellette County. Observed by H. C. Hampton. Recorded by Richard Adrian.

124. Fall — one — ½ mile south of Blunt, Hughes County. Found dead on road by A. M. Giziewski. Recorded by F. Robert Henderson.

125. September 22 — one — U. S. Highway 16, eastern Jones County. Observed in prairie dog town along road by James O. Lee, Jr.

126. Winter — one — T 15 N, R 1 E, Harding County. Found dead in trap in prairie dog town during blizzard by hired hand of Dahlen brothers. Recorded by Douglas R. West and Donald F. Fortenbery.

127. December — one — T 40 N, R 30 W, Mellette County. Shot by rabbit hunter at night. Recorded by Richard Adrian.

1964

128. 1964 — one — T 20 N, R 3 E, Harding County. Observed in prairie dog town by Joe Painter. Recorded by F. Robert Henderson.

129. May — pair — 6 miles southeast of Timber Lake, Dewey County. Observed in prairie dog town by Dallas G. Ingles.

130. Summer — one — T 43 N, R 37 W, Washabaugh County. Observed in abandoned prairie dog town by Louis Herscher. Recorded by F. Robert Henderson and Richard Adrian.

131. Summer — one — about 6 miles west of Cottonwood, Pennington County. Observed in road ditch by Frank Pratt. Recorded by F. Robert Henderson.

132. Summer — one — T 40 N, R 33 W, along Washabaugh - Mellette County line. Shot along road by Marvis Littier. Recorded by F. Robert Henderson.

133. Summer — one — T 41 N, R 37 W, Washabaugh County. Observed crossing road by Charles Vogelgesang. Recorded by F. Robert Henderson.

134. June — four to six — T 98 N, R 72 W, Gregory County. Nest of young ferrets plowed under in old corn field by Lloyd Gilbert. Recorded by Richard Adrian and F. Robert Henderson.

135. June — one — T 1 S, R 17 E, Pennington County. Observed in prairie dog town by Peder Kjerstad. Recorded by Richard Adrian and F. Robert Henderson.

136. About July 1 — one — T 13 N, R 22 E, Dewey County. Observed in small prairie dog town by Rock Cowan. Recorded by Dale Wade.

137. July — one — T 102 N, R 78 W, Tripp County. Shot in hayfield by James Calhoon. Recorded by Richard Adrian and F. Robert Henderson.

138. July — two — T 97 N, R 74 W, Tripp County. Observed in hayfield by Louis Laprather. Recorded by F. Robert Henderson and Richard Adrian.

139. July — one adult and four young — southeast of Longvalley, Washabaugh County. Observed crossing road near prairie dog town at night by Frank Schramer, Jr. Recorded by F. Robert Henderson and Richard Adrian.

140. July — one — T 40 N, R 40 W, Washabaugh County. Observed at edge of prairie dog town by Dan May. Recorded by F. Robert Henderson and Richard Adrian.

141. August — one — T 98 N, R 76 W, Tripp County. Observed near farm house by Dan McCabe. Recorded by F. Robert Henderson and Richard Adrian.

142. August — one — T 42 N, R 33 W, Mellette County. Observed crossing road at night by Burrell Phipps. Recorded by F. Robert Henderson and Richard Adrian.

143. August — four — T 20 N, R 12 E, Perkins County. Observed during haying by Mrs. Woodrow Lewton and son, 8 miles from prairie dog town. Recorded by Douglas R. West.

144. August 7 — one — T 40 N, R 31 W, Mellette County. Observed in prairie dog town at 1:30 p.m. by William Pullins and Richard Adrian. One observed previously in summer 1963 by Bryan Provancial. Recorded by Richard Adrian.

145. August 17 — one — T 40 N, R 31 W, Mellette County. Observed in prairie dog town (different from above) by Bryan Provancial. One adult and four young seen next day by Richard Adrian.

146. Fall — one — T 41 N, R 41 W, Shannon County. Found dead in trail along creek near prairie dog town by Indian. Reported by Lynn Montgomery.

147. Fall — two — along White River, 15 miles south of Kennebec, Lyman County. Came out of haystack being moved. Observed by Kenneth E. Christensen. Recorded by Walter H. Kittams.

148. September — one — T 101 N, R 78 W, Tripp County. Observed in dry lake bed by Raymond Abbey. Recorded by F. Robert Henderson and Richard Adrian.

149. September — one — T 100 N, R 78 W, Tripp County. Shot in prairie dog town by Gust Johnson. Recorded by F. Robert Henderson and Richard Adrian. Skin, S. D. State University.

150. September — one — T 99 N, R 77 W, Tripp County. Observed along creek by Ivan Fischer. Recorded by F. Robert Henderson and Richard Adrian.

151. September — one — T 3 N, R 21 E, Haakon County. Observed crossing road by R. L. McIlravy. Recorded by F. Robert Henderson and Richard Adrian.

152. September — one — 8 miles northeast of New Underwood, Meade County. Observed in prairie dog town by Marllon Carter. Recorded by F. Robert Henderson.

153. October — one — T 96 N, R 72 W, Gregory County. Observed along creek by Adolf Bruntz. Recorded by F. Robert Henderson and Richard Adrian.

154. October — one — T 42 N, R 36 W, Washabaugh County. Observed along creek by Loras Riggins. Recorded by F. Robert Henderson and Richard Adrian.

155. October 7 — male — T 41 N, R 37 W, Washabaugh County. Found shot along road near prairie dog town. Recorded by F. Robert Henderson and Richard Adrian. Specimen mounted, Badlands National Monument. Viscera, S. D. State University.

156. October 20 — one — T 40 N, R 31 W, Mellette County. Observed in prairie dog town by Richard Adrian.

157. November — one — T 104 N, R 74 W, Lyman County. Observed in chicken house by Mrs. Harry Roth. Recorded by F. Robert Henderson and Richard Adrian.

158. November 9 — one — T 2 S, R 23 E, Jackson County. Observed at dusk along creek about 1 mile from prairie dog town by A. Orville Sandall.

159. Winter — one — T 20 N, R 4 E, Harding County. Observed in prairie dog town by John Niemi. Recorded by Douglas R. West.

1965

160. 1965 — one — eastern Pennington County. Observed in prairie dog town by Carroll Knutson. Recorded by F. Robert Henderson.

161. About 1965 — one — 4 miles south of Kennebec, Lyman County. Found dead on road by Kenneth E. Christensen. Recorded by Walter H. Kittams.

162. March — one or more — T 44 N, R 33 W, Washabaugh County. Observed in prairie dog town by Art Thode. Recorded by Paul F. Springer.

163. April — one — T 2 N, R 24 E, Haakon County. Observed in old culverts in farm yard by Mrs. John Larsen. Recorded by F. Robert Henderson and Richard Adrian.

164. April — one — Wayne Everidge ranch northeast of Black Horse Butte Creek, Corson County. Observed in prairie dog town by Dallas G. Ingles.

165. April 2 — one — T 41 N, R 31 W, Mellette County. Observed in prairie dog town at 11:00 a.m. by James Carr. Recorded by F. Robert Henderson and Richard Adrian. One adult and five young observed July 12, 1966, by Conrad Hillman and James Carr.

166. April 15 — one — T 5 N, R 20 E, Haakon County. Observed in haystack by William Hespe. Recorded by F. Robert Henderson and Richard Adrian.

167. April 22 — one — T 39 N, R 30 W, Todd County. Observed in prairie dog town by Jack Knipel. Recorded by Richard Adrian.

168. Late April or early May — one — T 16 N, R 16 E, Perkins County. Observed by Kelvin Englehart. Recorded by Paul F. Springer.

169. May 1 — one — T 1 S, R 22 E, Jackson County. Observed in prairie dog town carrying snake into burrow at night by Hollis Young. Recorded by F. Robert Henderson.

170. May — one — T 42 N, R 35 W, Washabaugh County. Observed running across road from prairie dog town to alfalfa field by Stanley Barber. Recorded by F. Robert Henderson.

171. May — one — T 38 N, R 41 W, Shannon County. Observed in prairie dog town by Tony Englebert. Recorded by Richard Adrian and F. Robert Henderson.

172. Summer — one — T 17 N, R 8 E, Harding County. Observed in 160-acre prairie dog town by William Wammer. Recorded by Douglas R. West.

173. Summer — one — T 41 N, R 37 W, Washabaugh County. Observed near creek in daytime by Charles Vogelgesang. Recorded by F. Robert Henderson.

174. Summer — one — Kyle, Shannon County. Killed by Leroy Apple near his house. Recorded by F. Robert Henderson.

175. Summer — one — T 5 N, R 12 E, Meade County. Observed in 20-acre prairie dog town by Harry Snook. Recorded by Douglas R. West.

176. Summer — one — T 7 N, R 14 E, Meade County. Observed in prairie dog town by Slim Carney. Recorded by Douglas R. West.

177. Early June — one — T 39 N, R 34 W, Bennett County. Observed in prairie dog town by W. D. Good. Recorded by F. Robert Henderson and Richard Adrian.

178. June — one — T 40 N, R 33 W, Washabaugh County. Observed running under haystack by Russell Allard. Recorded by Richard Adrian.

179. Early July — eight — T 119 N, R 70 W, Faulk County. Observed in Richardson ground squirrel colony by Robert Schilder. Recorded by Paul F. Springer.

180. July — one — T 40 N, R 39 W, Washabaugh County. Observed crossing road in daytime by David Jones. Recorded by F. Robert Henderson.

181. July — one — near Crow Lake, Jerauld County. Observed in prairie dog town by C. F. Gunderson. Recorded by F. Robert Henderson.

182. Last half of July — one — T 2 S, R 5 E, Custer County, elevation 5800 - 6000 feet. Observed running along road by John Clark. Recorded by Paul F. Springer.

183. August — one — along Bull Creek, 7 miles east of Hamill, Lyman County. Observed in prairie dog town by Ralph Block.

184. August or September — one — T 10 N, R 21 E, Ziebach County. Observed in prairie dog town by Ed Bickel. Recorded by Paul F. Springer.

185. August 8 — one — T 38 N, R 47 W, Shannon County. Observed in 160-acre prairie dog town by Levi Good Voice Flute. Recorded by A. Lorin Ward.

186. August 12 — young male — T 40 N, R 32 W, Mellette County. Found dead in trap in prairie dog town by Otto Huber. Recorded by Richard Adrian. Decomposed carcass with skull, S. D. State University.

187. September 29 — adult female — T 2 N, R 19 E, Haakon County. Killed at night by domestic dog in ranch yard. Observed by Marvin Eide. Recorded by F. Robert Henderson. Skin and carcass, S. D. State University.

188. October — one — T 40 N, R 34 W, Washabaugh County. Observed crossing road at night by Joe Williams. Recorded by F. Robert Henderson.

189. October — one — T 17 N, R 19 E, Ziebach County. Observed in ravine by Ed Bickel. Recorded by Paul F. Springer.

190. October 10 — male — U. S. Highway 16, T 2 S, R 20 E, Jackson County. Found dead on road in early morning by F. Robert Henderson. Skin, S. D. State University.

191. October 21 — one — T 42 N, R 32 W, Mellette County. Observed in prairie dog town by A. Orville Sandall.

192. Winter — one — near Cherry Creek, Ziebach County. Observed in 160-acre prairie dog town by George Alfilich. Recorded by Robert Burgee.

1966

193. January — one — 2 miles southeast of Hisle, Washabaugh County. Observed in prairie dog town by Pat Weaver. Recorded by F. Robert Henderson.

194. Late winter and early spring — one — T 41 N, R 36 W, Washabaugh County. Observed several times in oats strawstack, 1 mile from prairie dog town by P. W. Kattenbach. Recorded by A. Orville Sandall and F. Robert Henderson.

195. Spring — one — T 38 N, R 47 W, Shannon County. Observed in prairie dog town at night by Russell Loud Hawk. Recorded by F. Robert Henderson.

196. March 7 or 8 — adult male — T 38 N, R 26 W, Todd County. Killed by domestic dogs. Observed by William Abbott. Recorded by F. Robert Henderson. Skeleton in F. Robert Henderson Collection.

197. March 24 — one — T 40 N, R 31 W, Mellette County. Observed in prairie dog town at 1:00 a. m. by F. Robert Henderson and Donald K. Fortenbery.

198. April 13 — one — Tuthill, Bennett County. Observed standing along road at 8:30 p.m. by Donald G. Young.

199. May — one — T 19 N, R 15 E, Perkins County. Observed in prairie dog town by Constant Schell. Recorded by Douglas R. West.

200. May — one — T 3 S, R 31 E, Jones County. Killed by domestic dog. Observed near prairie dog town by Herman Hendrick. Recorded by F. Robert Henderson.

201. May 2 — two — T 43 N, R 32 W, Mellette County. Observed in prairie dog town between 2:30 and 6:40 a.m. by Conrad Hillman.

202. Summer — one — T 7 N, R 20 E, Haakon County. Observed in prairie dog town by Emery Markwed. Recorded by F. Robert Henderson.

203. Summer — two — T 40 N, R 30 W, Mellette County. Observed in prairie dog town by Richard Adrian.

204. September 12 — young female — White River, Mellette County. Shot and given to William Pullins. Specimen 289498, U. S. National Museum. Carcass, S. D. State University.

205. September 19 — one — White River, Mellette County. Observed running under a porch by Buddy Hutchinson. Recorded by William Pullins.

206. October — one — T 42 N, R 32 W, Mellette County. Observed in prairie dog town by school teacher. Observed October 7 by Conrad Hillman.

207. October 11 — one — T 42 N, R 30 W, Mellette County. Observed in prairie dog town by William Pullins.

208. October 21 — one — T 42 N, R 32 W, Mellette County. Observed in prairie dog town by A. Orville Sandall.

209. Late fall — one — northwest of Milesville, Haakon County. Observed along a creek by Donald Loobey. Recorded by F. Robert Henderson.

1967

210. Spring — one — T 2 N, R 25 E, Haakon County. Observed several times in prairie dog town by William Donovan. Recorded by F. Robert Henderson.

211. March 9 — one — T 40 N, R 34 W, Washabaugh County. Observed in prairie dog town at 7.30 a.m. by F. Robert Henderson.

212. April 29 — adult female — U. S. Highway 18, T 37 N, R 39 W, Bennett County. Found dead on road at 2:00 a.m., 3 miles from prairie dog town by Jasper Milk. Recovered by F. Robert Henderson. Mounted specimen, Pine Ridge Indian Reservation, Pine Ridge, S. D. Carcass with skull, S. D. State University.

213. May — one — T 3 S, R 15 E, Pennington County. Observed along road 1 mile from prairie dog town by Louis Blumer. Recorded by Donald K. Fortenbery.

214. May 9 — one — T 42 N, R 30 W, Mellette County. Observed crossing road at 9:30 p.m. by Mrs. James Carr.

215. May 16 — adult female — U. S. Highway 83, T 3 S, R 29 E, Jones County. Chased by great horned owl onto road adjacent to prairie dog town and run over by Dale Richardson at 3:00 a.m. Recorded by F. Robert Henderson. Mounted specimen, S. D. Department Game, Fish and Parks. Carcass with skull, S. D. State University.

216. May 17 — one — T 41 N, R 30 W, Mellette County. Observed in prairie dog town at 12:10 a.m. by Conrad Hillman.

217. Summer — one — 5 miles north of Sharps Corner, Shannon County. Observed by Bill Lone Bear. Recorded by F. Robert Henderson.

218. Summer — one — T 36 N, R 45 W, Shannon County. Observed by George Swift Bird. Recorded by F. Robert Henderson.

219. June 29 — one — T 42 N, R 40 W, Washabaugh County. Observed crossing road near prairie dog town at 9:00 p.m. by F. Robert Henderson, Thomas Kuck, and David Linde.

220. July or August — two — along U. S. Highway 212, 5 miles east of Faith, Ziebach County. Observed by Mrs. Dono Capp. Recorded by Douglas R. West.

221. July 7 — one — T 124 N, R 78 W, Walworth County. Observed in 25-acre prairie dog town by Walter Larsen.

222. July 18 — one — Interstate 90, 1 mile east of New Underwood, Pennington County. Observed crossing road by Jack Hansen. Recorded by B. J. Rose.

223. August 2 — adult and four young — 1 mile southwest of White River, Mellette County. Observed in 10-acre prairie dog town by Raymond L. Linder and Donald K. Fortenbery.

224. September 5 — young male — on S. D. Highway 40, 3 miles west of White River, Mellette County. Run over on road by Jerry Krogman. Recorded by Conrad Hillman. Specimen at S. D. State University.

225. Late November — one — T 19 N, R 1 E, Harding County. Observed in prairie dog town by Lowell Cordell. Recorded by Paul F. Springer.

SCIENTIFIC NAMES OF ANIMALS AND PLANTS

MAMMALS

Badger **(Taxidea taxus)**
Bison **(Bison bison)**
Black-footed ferret **(Mustela nigripes)**
Black-tailed prairie dog **(Cynomys ludovicianus)**
Bobcat **(Lynx rufus)**
Coyote **(Canis latrans)**
Desert cottontail **(Sylvilagus auduboni)**
Domestic cat **(Felis catus)**
Domestic dog **(Canis familiaris)**
European fitch ferret or European polecat **(Mustela putorius)**
Golden-mantled squirrel **(Citellus lateralis)**
Long-tailed weasel **(Mustela frenata)**
Mink **(Mustela vison)**
Pronghorn **(Antilocapra americana)**
Richardson ground squirrel **(Citellus richardsoni)**
River otter **(Lutra canadensis)**
Short-tailed weasel **(Mustela erminea)**
Striped skunk **(Mephitis mephitis)**
Thirteen-lined ground squirrel **(Citellus tridecemlineatus)**
White-tailed jackrabbit **(Lepus townsendi)**
White-tailed prairie dog **(Cynomys gunnisoni)**

BIRDS

Burrowing owl **(Speotyto cunicularia)**
Golden eagle **(Aquila chrysaetos)**
Great horned owl **(Bubo virginianus)**
Horned lark **(Eremophila alpestris)**
Killdeer **(Charadrius vociferus)**
Rough-legged hawk **(Buteo lagopus)**
Snowy owl **(Nyctea scandiaca)**
Western meadowlark **(Sturnella neglecta)**

REPTILES

Bull snake **(Pituophis melanoleucus)**
Prairie rattlesnake **(Crotalus viridis)**

INSECTS

Carolina locust **(Dissosteira carolina)**
Prairie dog flea **(Opisocrostis hirsutus)**

PLANTS

Blue grama **(Bouteloua gracilis)**
Buffalo grass **(Buchloe dactyloides)**
Green needlegrass **(Stipa viridula)**
Western wheatgrass **(Agropyron Smithii)**

The University of Notre Dame

Prairie Dog Distribution in Areas Inhabited by Black-Footed Ferrets
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Prairie Dog Distribution in Areas Inhabited by Black-footed Ferrets

ABSTRACT: The distribution of black-tailed prairie dog *(Cynomys ludovicianus)* towns was delineated in a 1490 km^2 study area in Mellette County, South Dakota, and was examined to determine the characteristics of black-footed ferret *(Mustela nigripes)* habitat. Between 1964 and 1974, black-footed ferrets were observed on 14 prairie dog towns in this area. Eighty-six prairie dog towns, located throughout the study area, were not randomly distributed; towns were paired or clumped in spatial distribution. Mean distance between a town and its nearest neighbor was 2.4 km; mean distance between a ferret-occupied town and the nearest town was similar, 2.7 km. Management recommendations are to maintain at least eight towns per township, each at least 12 ha in size. Of these eight towns, two or more should exceed 40 ha.

INTRODUCTION

The black-footed ferret, an endangered species, has been the subject of intensive study in Mellette Co., South Dakota, since the discovery of a family group there in 1964 (Hillman, 1968; Henderson *et al.,* 1969; Sheets *et al.,* 1972; Linder *et al.,* 1972; Hillman and Linder, 1973). Ferrets observed during those studies inhabited 14 black-tailed prairie dog towns. No ferrets were observed off towns with the exception of those killed on roads, killed by dogs or shot. Ferrets were seen away from prairie dog towns by ranchers and other local people, but none of these reports was verified.

Black-footed ferrets feed mainly on prairie dogs; they utilize prairie dog burrows for denning sites and shelter, and remain on the same prairie dog town for indefinite periods of time (Hillman, 1968; Sheets *et al.,* 1972). Ferrets were observed on prairie dog towns in Mellette County each year from 1964 to 1974, but population censuses were impossible because of the ferret's nocturnal and secretive habits.

The purpose of this paper is to describe characteristics and spatial distribution of prairie dog towns in ferret-occupied areas. This information may be helpful to land managers attempting to preserve prairie dog towns as ferret habitat.

METHODS AND STUDY AREA

Prairie dog towns (located by aerial surveys, interviews with landowners and examination of U.S. Soil Conservation Service aerial photos) were plotted on topographic and county maps. Surveys to locate ferrets were conducted periodically on prairie dog towns by methods previously described by Henderson *et al.* (1969) and Hillman (1968). Only those ferrets actually sighted were included.

The 1490 km^2 study area in western Mellette Co., South Dakota, is within the White River drainage basin (Fig. 1). Topography consists of rolling grasslands interspersed with small creeks, brushy draws and river breaks; badlands occur in the western part. Eighty-two percent of the land area in the county is rangeland; cattle ranching is the primary enterprise (White, 1975).

Soils in the area are from the Norrest, Huggins-Kadoka, Imlay-Conata-Badlands, and Opal-Promise-Samsil associations; they are derived from clayey shales of the Pierre formation (White, 1975). The climate is characterized by hot summers and cold winters. Mean annual temperature is 8 C, and average annual precipitation is 43 cm, 75% of which occurs during April through September (Westin *et al.,* 1959).

Prairie dog towns were chiefly on lands owned or leased by operators of large ranches. In most instances, ranchers were tolerant of prairie dogs if their numbers were not allowed to increase. Several landowners were sympathetic toward this study and withheld treatment of towns that were inhabited by ferrets. Approximately 40% of the towns were on Indian lands. The Rosebud Sioux Tribe has not had an active prairie dog control program in the area since 1965.

RESULTS AND DISCUSSION

From 1966 to 1973 prairie dog control programs were limited, a few new prairie dog towns appeared, and expansion of towns was not extensive. Seven towns (146 ha) were treated under government-supervised programs in 1966-1969, but the only control in 1970-1973 was practiced by landowners. Extensive ferret surveys were conducted in the study area during this period (Hillman and Linder, 1973). Since 1973, prairie dog towns have expanded, but no accurate count of new towns or towns poisoned by landowners has been possible. This information also was lacking for years prior to 1966.

Eighty-six prairie dog towns were located and mapped (Fig. 1) on four topographic sites. Towns ranged in size from 2-120 ha. Thirty towns (35%) were on benches or terraces adjacent to a creek or floodplain, 30 towns (35%) occurred in rolling hills of slope greater than 5%, 20 (23%) were on "flats" and six towns (7%) were in badland areas. Occasionally, larger towns occurred on a combination of two topographic situations.

Prairie dog towns commonly occurred near rivers or creeks throughout western South Dakota and much of the Great Plains region (Koford, 1958). In 1974, 83 towns occurred on a strip 1-6 km wide along 160 km of the White River in Shannon Co., South Dakota. Towns were also numerous near the Cheyenne and Belle Fourche rivers and their tributaries. River or creek bottom sites in Mellette County are characterized by deep, fine-to-medium-textured alluvial soils. Trees and small shrubs are common on floodplains. Prairie dogs occupied benches which rarely exceeded a 5% slope. They occupied lower lands in level, unwooded oxbows along major drainages with wide floodplains. These sites were subject to occasional flooding.

Prairie dog towns also were common in draws or swales in rolling grasslands. Nine of 30 towns in this type occurred in the upper end or grassy bowls of minor tributaries. Other grassland towns occurred in shallow depressions, gently rolling hills or on hillsides. Many towns were associated with abandoned farm buildings, windmills and stock ponds.

Twenty towns occurred on relatively flat land in lowlands or on high prairie terraces. Panspots or alkaline areas frequently were inhabited by prairie dogs on the lowlands. Prairie dogs occupied high, prairie terraces which previously were farmed; several of these towns were poisoned and plowed since 1973.

Six prairie dog towns occurred in badland areas. They occupied grassy plateaus adjacent to or between deep, dry creekbeds. Two towns occurred in shallow, dense-clay sites formed from erosion of adjacent badland buttes. Steep-sided, barren outcroppings limited the expansion of most badland towns; generally, badlands are unsuitable for prairie dogs.

Several large tracts of rough terrain, steep canyons and river breaks within the study area were not occupied by prairie dogs. Throughout the study area, towns were repeatedly poisoned in past years, and many were not reoccupied.

Black-footed ferrets occupied 14 towns in the four sites in relative proportion to the number of towns that occurred in each type; four were near creeks, five in rolling grasslands, four were on flatland and one was in a badland area.

Unlike some members of the weasel family, ferrets are believed to kill only enough to eat. A town (14 ha) occupied by ca. 52 prairie dogs in June 1966 was occupied by a single ferret for

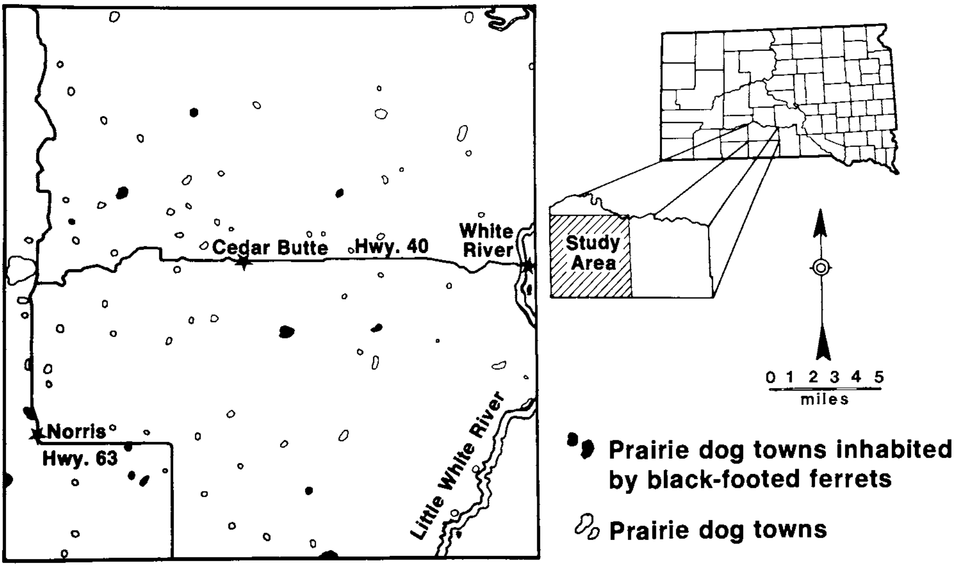

Fig. 1.—Black-footed ferret study area in western Mellette Co., South Dakota

6 months, but prairie dog numbers were not severely reduced. By autumn 1967 prairie dogs were more abundant than in 1966 on that town (Hillman, 1968). Prairie dog numbers were not markedly reduced on 12 other towns inhabited by one or two ferrets for portions of a year.

The larger towns may be more important for adult female ferrets rearing young. Of 11 litters observed, six occurred on four towns that equaled or exceeded 40 ha (40, 43, 57 and 120 ha). These towns were considerably larger than the average of 8 ha as recorded for 151 towns throughout Mellette County (Linder *et al.,* 1972). The sizes of towns occupied by the other five litters were 10, 12, 13, 13 and 16 ha, all larger than average. Obviously, a greater food supply is required for a family group of ferrets. Numbers of prairie dogs declined on portions of one town frequented by ferrets, but, generally, total numbers of prairie dogs were not greatly reduced on towns occupied by litters (Hillman and Linder, 1973).

We used procedures for demonstrating the occurrence of nonrandom distribution in populations given by Clark and Evans (1954). Although prairie dog towns occurred throughout the study area, they were not randomly distributed. The spatial relationship was a clumped or paired distribution.

The mean distance between a town and its nearest neighboring town was 2.4 km; the distance between a town occupied by ferrets and its nearest neighboring town (2.7 km) was similar. Mean numbers of towns per km^2 that occurred in 1.6-km-wide bands (mile-wide bands) away from towns occupied by ferrets were 0.47, 0.37, 0.45 and 0.29; these were not different ($P>0.05$). The mean distance between towns inhabited by ferrets was 5.4 km (range 1.0-11.1).

Prairie dogs are now more abundant in Mellette County than 6 years ago, but ferret observations have not increased proportionally. Prairie dogs also are more abundant in other areas of South Dakota, yet ferrets have not been seen in these areas in recent years.

Because of the limited understanding of ferret habitat needs, the following recommendations should be interpreted as meeting only minimal habitat requirements: (1) maintain at least eight towns per township; (2) each town should be at least 12 ha in size; and (3) two or more towns should exceed 40 ha. These recommendations are based on data from our study area, where ferrets have been known to survive over a period of years.

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LITERATURE CITED

CLARK, P. J. AND F. C. EVANS. 1954. Distance to nearest neighbor as measure of spatial relationships in populations. *Ecology,* **35**:445-453.

HENDERSON, F. R., P. F. SPRINGER AND R. ADRIAN. 1969. The black-footed ferret in South Dakota. *S.D. Dep. Game, Fish Parks Bull.,* Pierre. 37 p.

HILLMAN, C. N. 1968. Field observations of black-footed ferrets in South Dakota. *Trans. N. Am. Wildl. Nat. Resour. Conf.,* **33**:433-443.

——— AND R. L. LINDER. 1973. The black-footed ferret, p. 10-23. *In:* Trans. Black-footed ferret-prairie dog workshop. South Dakota State Univ., Brookings.

KOFORD, C. B. 1958. Prairie dogs, whitefaces, and blue grama. *Wildl. Monogr. 3.* 78 p.

LINDER, R. L., R. B. DAHLGREN AND C. N. HILLMAN. 1972. Black-footed ferret-prairie dog interrelationships, p. 22-37. *In:* Symposium on rare and endangered wildlife of the southwestern United States. New Mexico Dep. Game, Fish, Santa Fe.

SHEETS, R. G., R. L. LINDER AND R. B. DAHLGREN. 1972. Food habits of two litters of black-footed ferrets in South Dakota. *Am. Midl. Nat.,* **87**:249-251.

WESTIN, F. C., L. R. PUHR AND G. J. BUNTLEY. 1959. Soils of South Dakota. *S.D. State Univ. Agric. Exp. Stn. Soil Surv. Ser. 3.* 34 p.

WHITE, E. M. 1975. Soil Survey of Mellette County, South Dakota. U.S. Dep. Agric. Soil Cons. Serv. 112 p.

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Bison Versus Cattle: Are They Ecologically Synonymous?

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Abstract

Historically, the plains bison (*Bison bison* Linnaeus) was the most numerous and influential grazer on the Great Plains. Today 500 000 bison occupy North America among more than 100 000 000 cattle. In an attempt to restore their historical ecological role, bison are translocated onto landscapes previously manipulated for cattle use through water and fence development. We hypothesized that bison would use these landscapes similarly to cattle, thus maintaining homogenous grazing and reducing the restoration potential of bison at a landscape scale. We quantified differences between bison populations at different locations and spatial scales (American Prairie Reserve, Malta, Montana, USA, and Grasslands National Park, Val Marie, Saskatchewan, Canada, 2010–2011) and bison and cattle at similar locations and spatial scales using behavioral observations, movement analyses, and resource selection functions. Bison and cattle differed in all behaviors (grazing, standing, bedded, moving, other); however, landscape attributes resulted in behavior differences within species. Cattle spent a higher proportion of time grazing (45–49%) than bison (26–28%) and increased time at water. Bison moved at a 50–99% faster rate than cattle, and first passage time movement analyses identified selection of bison foraging patches (11 690 ha) larger than cattle foraging patches (48–615 ha). Similar to cattle, bison avoided most vegetation communities in relation to riparian communities and selected areas closer to water. Cattle selected for high plant biomass, whereas bison selected for intermediate plant biomass. This study has implications when bison and cattle are used to meet prairie restoration objectives. For bison, large landscapes that include variation in topography and vegetation communities are required. Furthermore, limiting manmade water sources may facilitate bison grazing patterns that more closely approximate historical bison use. For livestock, reduced movement and increased time spent grazing encourage grazing practices that increase heterogeneous grazing at a pasture scale.

Key Words: behavior, first-passage time, grazing, heterogeneity, resource selection, water

INTRODUCTION

The near extinction and subsequent recovery of plains bison (*Bison bison* Linnaeus) throughout North America was the first and greatest conservation success in North America (Sanderson et al. 2008). Today ~500 000 bison occupy North America because of the cooperation of private individuals, nonprofit organizations, and the federal governments of the United States, Canada, and Mexico. Despite the numerical recovery of the species, recent questions have surfaced regarding the ecological success of these efforts because fewer than 21 000 plains bison are managed as conservation herds (i.e., not for commercial use; $n=62$). Thirteen percent ($n=8$) of conservation herds are outside of their historical range, 92% ($n=57$) have fewer than 1 000 individuals, and only 8% ($n=5$) are managed on areas of more than 2 000 km^2 (Gates et al. 2010). In comparison, more than 95% of bison are in commercial production and are subjected to animal husbandry practices (e.g., altered sex:age ratios, unnatural growth performance, reduced mate competition), which may result in irreversible changes to morphology, physiology, and behaviors (Freese et al. 2007) that alter their ecological influence on the landscape. The collective effect of ecological alterations and issues such as disease (Aune and Gates 2010) and domestic cattle gene introgression (Halbert and Derr 2007) can prohibit the mixing of commercial and conservation herds because of different management and conservation goals. As a result, many conservation groups and state and federal agencies are questioning the ecological significance of replacing historic bison populations with domestic cattle at a landscape scale.

Historically, bison were the dominant grazer throughout the Great Plains, affecting vegetation communities through grazing, physical disturbance, nutrient cycling, and seed dispersal (McHugh 1958; Knapp et al. 1999). These activities contributed to grassland heterogeneity that supported many prairie obligate species (e.g., grassland songbirds) in the tall, mixed, and short grass prairie (Fuhlendorf et al. 2006; Powell 2006; Gates et al. 2010). Following the reduction of the bison herds, bison were replaced by domestic cattle, and a significant shift occurred, resulting in overgrazing and then rotational grazing regimes. Contemporary range management practices are

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designed to maximize livestock production through cross-fencing and uniformly distributed stock reservoirs, effectively rescaling the grazing process across the landscape in a homogenous fashion (Fuhlendorf and Engle 2001; Derner et al. 2009).

Today livestock numbers on rangelands in the United States and Canada are two times higher than historical bison estimates,[1] yet there are few studies comparing the ecological similarities between introduced livestock and bison, particularly when managed as wild populations on large, complex landscapes (Fuhlendorf et al. 2010). Bison and cattle demonstrate fundamental ecological differences in habitat use (van Vuren 1983; Allred et al. 2011), forage use (Peden et al. 1974; Plumb and Dodd 1993; Towne et al. 2005), and behavior (Plumb and Dodd 1993). In addition, water requirements have been identified as a major difference between the species as cattle spend more time near water resources and riparian areas than bison (van Vuren 1983; Fuhlendorf et al. 2010). In particular, bison employ distinct travel patterns that include travel from general use areas (e.g., feeding, bedding) to watering areas where they spend minimal time and then return to general use areas (McHugh 1958; van Vuren 1979). However, only Allred et al. (2011) have explicitly tested for cattle selection and bison avoidance of riparian areas and water sources at a large spatial scale.

Data are available regarding the ecological differences between bison and cattle; however, direct comparisons between bison and cattle are difficult because of varying management practices (e.g., pasture size, stocking densities, management priorities, cattle breed) and confounding environmental factors (Plumb and Dodd 1993; Towne et al. 2005; Fuhlendorf et al. 2010). Fuhlendorf et al. (2010) reported nine studies that compared bison and cattle with an ecological focus, only two of which attempted to control for confounding effects. Recent work on the Tallgrass Prairie Reserve was the third study to control for confounding effects and the first to occur on pasture units over 300 ha (Allred et al. 2011).

Bison translocation efforts are occurring in the Northern Great Plains in areas previously manipulated for livestock (i.e., water development and fence construction). Because these translocation efforts are implemented beside domestic livestock operations, we were provided opportunities for side-by-side comparisons of bison and cattle. Furthermore, with multiple bison populations within the region, we were able to compare pasture attributes used by bison across differing vegetation communities and spatial scales. Thus, our objectives were to compare the behavior, movement, and resource use of bison and cattle on large pasture units ($> 1\,000$ ha) within the Northern Great Plains in an effort to make inferences regarding potential impacts on landscape heterogeneity. For this study, landscape hetero- and homogeneity refers to vegetation structure and composition at spatial scales of more than 1 000 km^2. Pasture attributes refer to topographic characteristics, vegetation communities, and management practices. We hypothesized that pasture attributes would influence the behaviors (e.g., standing, bedded, grazing, movement, and resource use) of bison and cattle. As such, we predicted bison and cattle in units with similar pasture attributes would demonstrate comparable behaviors reported in previous studies of smaller pasture units. We also predicted bison would differ in their ecological behaviors (e.g., movement, water use) when under different management structures, including pasture size and water density.

METHODS

Study Area

We compared bison and cattle in two study areas within the northwestern glaciated plain ecoregion (Forrest et al. 2004) of north-central Montana and southwestern Saskatchewan, Canada, in 2010 and 2011 (Fig. 1). In north-central Montana, we compared bison on the American Prairie Reserve (APR [67% public land]) and cattle on the Barnard Ranch (BR [65% public land]) and Weiderrick Ranch (WR [100% public land]). The APR (lat 47°45′48″N, long 107°41′43″W) is located 74 km south of Malta, Montana, and is adjoined on the east by BR (lat 47°43′00″N, long 107°38′00″W) and west by WR (lat 47°44′11″N, long 107°51′28″W). To compare bison across spatial scales, vegetation communities, and water availability, a second bison site was selected 150 km north in Grasslands National Park (GNP [Val Marie, Saskatchewan, Canada {lat 49°09′40″N, long 107°32′49″W}]).

Dominant plant species on APR, BR, and WR are representative of a sagebrush steppe system that includes blue grama (*Bouteloua gracilis* Griffiths), needlegrass (*Stipa* spp. Beauv), crested wheatgrass (*Agropyron cristatum* Gaertn), silver sagebrush (*Artemisia cana* Pursch), and Wyoming big sagebrush (*Artemisia tridentata* Nutt). Sedges (*Carex* spp.), cacti, and forb species are also common in the area. Dominant plant species in GNP are representative of the mixed-grass prairie ecosystems and include blue grama, needlegrass, western wheatgrass (*Pascopyrum smithii* Á Löve), and silver sagebrush.

Large ungulates on all sites include mule deer (*Odocoileus hemionus* Rafinesque), white-tail deer (*O. virginianus* Zimmermann), and pronghorn (*Antilocapra americana* Ord). Elk (*Cervus elaphus* Linnaeus) are common on all sites except GNP. Black-tailed prairie dogs (*Cynomys ludovicianus* Ord) and coyotes (*Canis latrans* Say) are common in all areas. Greater sage grouse (*Centrocercus urophasianus* Bonaparte), Baird's sparrows (*Ammodramus bairdii* Audubon), and mountain plover (*Charadrius montanus* Townsend) are grassland bird species of conservation concern found throughout the region.

The APR, BR, and WR lie in a semiarid region consisting of upland flats intersected by coulees and ephemeral streams flowing toward the Missouri River. Yearly precipitation ranges from 25.4–27.9 cm; however, 2010 and 2011 were 1.5–2.0 greater than the annual average (45.6 and 57.1 cm, respectively). Mean annual temperature is 6.5°C and ranges from –8.4°C in January to 20.8°C in July. Elevation ranges from 700 to 825 m. Soil primarily contains heavy clay loams with moderate amounts of salt resulting in high impermeability by water. Thus, most water developments remain full throughout the year.

The GNP also lies in a semiarid region and consists of similar topographic features as listed above. The Frenchman River

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[1] Fig. S1, available at http://dx.doi.org/10.2111/REM-D-12-00113.s1)

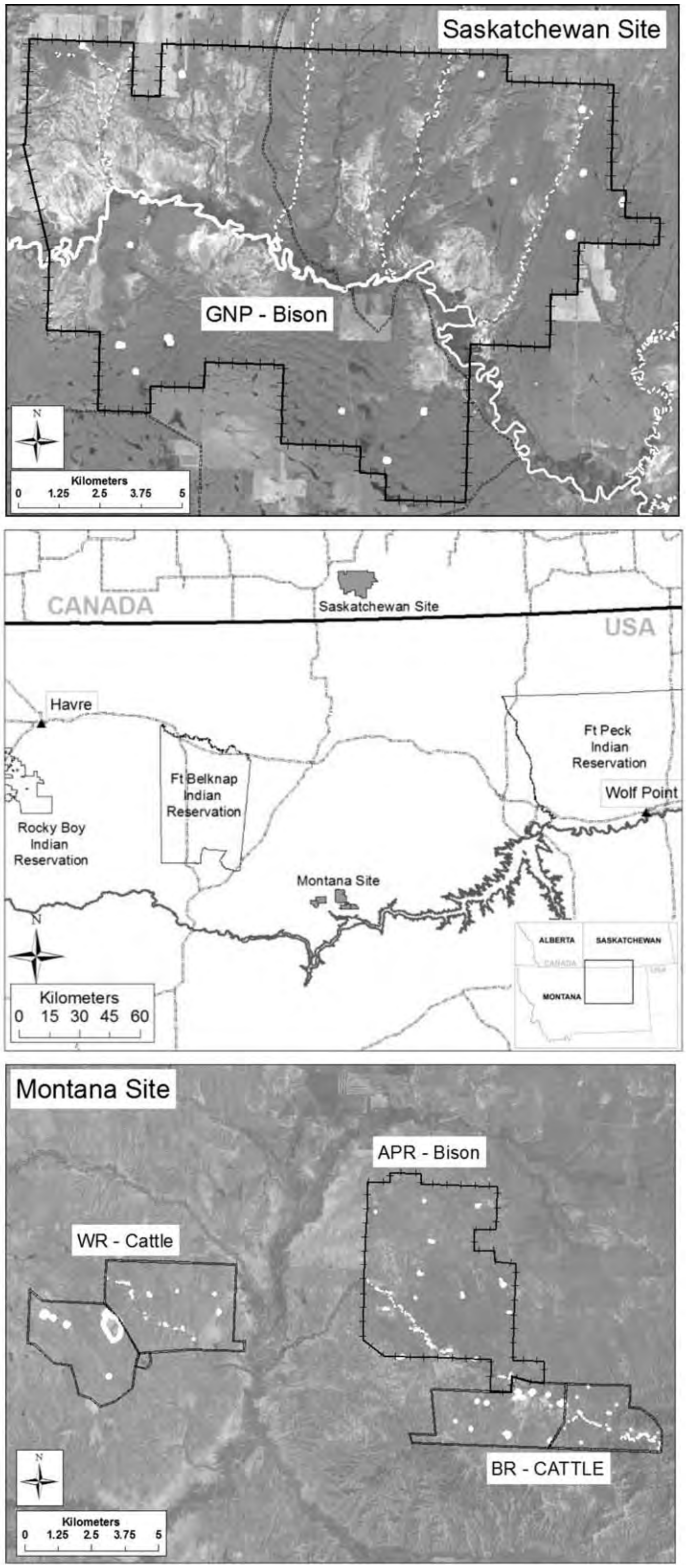

Figure 1. Location of bison and cattle study sites. Bison herds were located at American Prairie Reserve (APR; diamond) and Grasslands National Park (GNP; star). Two cattle herds are located in pastures adjacent to APR bison herd. White identifies man-made stock reservoirs and remnant pools within ephemeral streams. Dashed line identifies main ecotour route through GNP. Sites at APR are located 74 km south of Malta, MT, USA, and GNP is located 20 km southeast of Val Marie, SK, Canada.

runs through the southern section of the park with consistent, regulated flow throughout the year. Annual precipitation ranges from 30 to 33 cm; however, 2010 and 2011 were 1.4–2.0 times greater than average (46.5 and 53.1 cm, respectively). Mean annual temperature is 3.4°C and ranges from –13.4°C in January to 18.8°C in July. Elevation ranges from 750 to 900 m.

Bison on APR ($n=147$ in and 215 in 2010 and 2011, respectively) were contained within a 3 555 ha electrified pasture unit from 1 May through 31 October of each year (Fig. 1). The pasture contains 15 manmade reservoirs and an ephemeral stream that maintained small remnant pools during the study. Reynolds Hill Road passes through the eastern section of the APR, receiving low to moderate levels (~ 30 vehicles $\cdot$ d^{-1}) of use throughout the summer with heavier use (~ 250 vehicles $\cdot$ d^{-1}) during hunting season (1 September–25 November). Bison on GNP ($n=147$ and 195 in 2010 and 2011, respectively) were contained within an 18 153 ha pasture unit containing 26 reservoirs (Fig. 1); however, bison typically used only the northeast portion of the park during summer ($\sim 4\,200$ ha). This summer area contained five manmade reservoirs (three of which were permanent throughout summer), one large depression, and three ephemeral channels that contained remnant pools during the study. In addition to reservoirs, the Frenchman River provides water throughout the year, except when frozen. The main ecotour road passes through the center of the park ($\sim 6\,000$ visitors $\cdot$ yr^{-1}) from north to south and receives low to moderate levels of use throughout the summer, but recreational use is rare in the core summer range.

The WR grazed 100 cow/calf pairs (red and black Angus) from 1 July to 15 October on 2 rotational pastures (1 090 and 1 408 ha), that contained 5 to 7 reservoirs per pasture (Fig. 1). The BR grazed ~ 140 cow/calf pairs (Hereford and red Angus) on two rotational pastures (777 and 1 000 ha) that contained 6–8 reservoirs per pasture. The west BR pasture was bisected by Reynolds Hill Road. Stocking density was similar across APR and WR cattle pasture units but differed from BR pasture units (Table 1).

GPS Data Collection

We deployed Global Positioning System (GPS) radiocollars (Lotek 3300, Lotek 4400, Lotek Wireless Fish and Wildlife Monitoring, Newmarket, Ontario, Canada and NSG-LD2, North Star Science and Technology, LLC, King George, Virginia, USA) on adult female bison and cattle.[2] Bison were immobilized (A3080 and Xylazine; reversed with Naltrexone, or a mixture of Butorphanol-Azaperone-Medetomidine [BAM]; reversed with Naltrexone, Atipamezole and Tolazine, K. Kunkel, American Prairie Reserve, personal communication) by air-powered darts (Pneu-Dart, Williamsport, PA) fired from the ground. Cattle were physically restrained in a squeeze chute. Sixteen animals were instrumented in the study ($n=2$ on APR, $n=4$ on GNP, $n=5$ on BR, $n=5$ on WR), of which five individuals remained collared throughout the duration of the study ($n=2$ on APR, $n=3$ on GNP). Collars were scheduled to obtain locations every 1, 2, or 3 hr from collar deployment (1 June–9 July) till 31 August (or until collar failure) in 2010 and 2011.[3] The GPS locations were

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[2] Fig. S2, available at http://dx.doi.org/10.2111/REM-D-12-00113.s2

[3] Table S1, available at http://dx.doi.org/10.2111/REM-D-12-00113.s3

Table 1. Description of grazing pastures and stocking densities for animals owned by American Prairie Reserve (APR), Parks Canada (PC), Weiderrick Ranch (WR), and Barnard Ranch (BR). Analysis was performed on annual bison range (Park) and within summer home range (NE Corner) in Grasslands National Park (GNP). The GNP is located 20 km southeast of Val Marie, SK, Canada, and other sites are located 74 km south of Malta, Montana, USA.

Species	Owner	Pasture name	Year	AUM/ha
Bison	APR	APR	2010	0.25
			2011	0.18
	PC	GNP—Park Wide	2010	0.11
			2011	0.14
		GNP—NE Corner	2010	0.14
			2011	0.18
Cattle	WR	North	2010	0.14
			2011	0.09
		West	2011	0.16
	BR	East	2010	0.36
			2011	0.49
		West	2011	0.39

censored from analysis when APR bison moved outside of the designated pasture unit. This research was approved by the University of Montana Animal Care and Use Board (Animal Use Protocol No. 014-10PKWB) and Parks Canada (Permit No. GRA-2010-5415).

Landscape Variables

Abiotic variables (e.g., aspect, slope, and elevation) were developed from the 30×30 m Montana Digital Elevation Model and 15×15 m Canadian Digital Elevation Model. Biotic variables included vegetation community and 250×250 m Normalized Difference Vegetation Index data (NDVI [Moderate Resolution Imagine Spectroradiometer {Huete et al. 2002}]). Vegetation classifications on GNP were based on field work completed by ground sampling (R. Sissons, GNP, unpublished data). Landcover type was classified on APR, BR, and WR using remotely sensed data and was designed to allow for comparison between vegetation communities on GNP. We delineated 10 vegetation communities (eroded, upland grassland, disturbed, sloped grassland, riparian, valley grassland, treed, unclassified, sage-brush, and water bodies).[4] We used a dynamic measure of vegetation productivity by estimating primary productivity from midmonth NDVI estimates (Tucker and Sellers 1986). We analyzed anthropogenic variables using Euclidean distance estimates (km) for fence, water, and roads. We located permanent water sources using BLM (Malta Field Office, Malta, MT, USA) and Parks Canada (GNP Headquarters, Val Marie, Canada) topographic maps. We inspected water developments monthly to confirm water availability throughout summer. Additional water sources (e.g., hardpans, rainfall, drainages) are ephemeral pools (< 1 wk); thus we assumed they were homogenous throughout the pasture units and did not influence overall movement patterns of bison and cattle relative to permanent water sources.

Behavior

We conducted behavior observations of bison and cattle near semipermanent (< 3 mo) to permanent water sources to quantify the use of water by both species, and thus relate resource selection (see below) to water requirements. The distinct differences in use of watering areas by bison and cattle (van Vuren 1983; Fuhlendorf et al. 2010) allowed for inferences on the impact of variable water densities on landscape use by bison and the overall requirement of water by bison relative to cattle. Thus, we predicted time spent watering would differ between species (i.e., cattle > bison). We also predicted differences in time spent watering across bison sites (i.e., GNP > APR) due to GNP's decreased water availability in the northeast corner of the park, thus imitating a more historical water density.

Opportunistic behavioral observations were also recorded when groups of individuals were ≥ 25 m from water (25–1027 m). We assumed that at distances over 25 m, animals had not watered recently, and thus would make directed movements when watering was required. Observations (≤ 4 hr) occurred during daylight hours twice per day for one week per month per study group from 22 May–23 August 2010 and 2011. We were unable to collect observation data and watering events for 1.5 mo on the BR in 2010 due to the grazing rotation schedule and access was limited to WR in 2010 and 2011 due to weather conditions. This resulted in 87 behavioral observations ($n=34$ on APR, $n=29$ on GNP, $n=18$ on BR, $n=6$ on WR) spanning 155.3 hr and 544 watering events (i.e., the start of an adult animal drinking water), across all study areas ($n=200$ on APR, $n=185$ on GNP, $n=119$ on BR, $n=40$ on WR). Prewatering behavior of mixed groups (female, calf, and subadult males) was determined using instantaneous scan sampling (Altmann 1974) from distances over 100 m (Komers et al. 1992) and pooled across individuals within the sampling unit. A sampling unit consisted of a group of more than 2 animals separated from other groups by more than 100 m (range=2–224; median=38 [Fortin et al. 2003]) with multiple groups being observed concurrently if visible. Prior to watering events, behavior (grazing, standing, bedded, moving, other) of all individuals was recorded at 15 min intervals (Plumb and Dodd 1993). During the observation periods, individuals were also observed continuously for instances of watering events. When an individual animal began watering, the observation period (instantaneous scan samples) for all individuals ceased, and weather data (temperature, cloud cover, wind speed) and time spent at water (i.e., time in minutes from initial drinking activity to time when animal was more than one body length from water source) for each watering individual was recorded.

We calculated proportional differences in ecologically significant behaviors (i.e. moving, grazing). We used a χ^2 test to quantify whether behaviors differed among and within species. We used ANOVA to compare time spent at water between species and study locations. Lastly, a multiple analysis of variance (MANOVA) was used to calculate the influence of temperature on time spent at water. Statistical

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[4] Table S2, available at http://dx.doi.org/10.2111/REM-D-12-00113.s4

analyses were conducted using the Rcmdr package in R 2.15.1 (Fox 2005).

Movement

We predicted bison movement rates (MR), calculated from GPS data as distance (d) in meters (step length) divided by time (t) in seconds (fix interval), would be larger than those of cattle on pasture units of similar attributes due to increased resource (i.e., water) requirements by cattle. This would be expected if cattle were unable to travel large distances from water when physiologically constrained by higher summer temperatures and, thus, resulting in circular movements within a given radius of a watering source. In contrast, we expected bison to make linear movements away from water sources, which would result in greater movement rates. We also predicted bison on APR would demonstrate slower MR than bison on GNP due to reduced pasture units (i.e., fence construction). This would be expected if long-distance movements were inhibited by fence construction, thus decreasing the total distance traveled relative to a fix-interval. Movement rates had a non-normal distribution; thus we used a negative binomial regression to test this hypothesis. Analyses were performed in R 2.15.1 using the MASS package (Venables and Ripley 2002).

We used the first passage time (FPT) analyses to measure the search effort along a pathway (Fauchald and Tveraa 2003) to identify the spatiotemporal scale of biologically relevant movements (Turchin 1998; Morales et al. 2005). Specifically, FPT incorporates step length, turning angles, and tortuosity (Fauchald and Tveraa 2003) to estimate the spatial scale at which the consumer perceives a resource. Variance in FPT, calculated by the time it takes an animal to travel across a circle of a specified radius (Fauchald and Tveraa 2003), allows ecologists to distinguish area-restricted search behaviors from movement behaviors between patches.

FPT analyses were conducted in the adehabitatLT package of R 2.15.1 (Calenge 2006). Circles of radii between 50 and 15 000 m, increasing at 25 m increments, were applied to each GPS location along an individual movement path for bison and cattle. Location data were used from the focal sampling period (June–August 2010 and 2011) except for APR bison in 2011. The omission of 2011 data for APR bison was due to temporary bison movements outside of the designated pasture unit, which necessitated data censoring and resulted in an inadequate sample size for FPT analysis. For each GPS location along an individual movement path, we calculated the time spent moving along the path within a circle of a given radius. Where those circles intersected the movement path, we determined passage time of the resulting segment assuming constant rates of travel along interlocation steps. First passage times were not calculated in instances of missed locations which created breaks along the path (Williams et al. 2012). We evaluated the variation in passage time along each movement path using circles with radii ranging from 50 to 15 000 m at 25 m increments. Variation in FPT at each scale (circle radius) indicates the degree that movements are aggregated along the path. Because variation in FPT is expected to increase with increasing circle radii, variance in FPT was divided by the area of the circle (Frair et al. 2005; Williams et al. 2012) as a function of scale (circle radii), thus providing an indicator of the landscape scales to which individuals are responding for the summers of 2010 and 2011.

Resource Selection

We used a resource selection function (RSF) framework to compare resource use of bison and cattle during summer (1 June–31 August; Manly et al. 2002). Our specified covariates were vegetation community, water availability, and additional abiotic (elevation, aspect, slope), biotic (NDVI), and anthropogenic covariates (distance to roads, distance to fence) identified in previous bison and cattle resource selection studies. Because RSFs assume independence among observations (Hosmer and Lemeshow 2000), we used generalized linear mixed-models (GLMM) with a random-intercept for individual to allow for interpretation of selection among different populations and species (Hebblewhite et al. 2008; Bolker et al. 2009), thus accounting for temporal and spatial autocorrelation among individuals and groups (Breslow and Clayton 1993) and correcting for unbalanced number of locations among individuals (Bennington and Thayne 1994). Furthermore, data were pooled by month for each animal (i.e., Animal1_June2010, Animal2_June2010, Animal1_July2010, etc.) to provide a population estimate across the summer months while taking into account changing availability in our dynamic measure of vegetation productivity, NDVI.

We estimated RSFs at the third order scale (Johnson 1980) on APR, GNP, and cattle ranches. On APR and cattle pastures, we randomly sampled monthly availability ($n=1\,000$) across individual months within a given pasture for bison and cattle. In GNP we randomly sampled monthly availability ($n=1\,000$) within a 95% fixed kernel monthly home range (third order) using Geospatial Modeling Environment 6.0 (Beyer 2012). In GNP, we also estimated RSFs at a constrained second order scale (i.e., pasture unit) by randomly sampling monthly availability ($n=2\,000$) across the entire park to understand whether resource selection differed across spatial scales in GNP. We define this as constrained second order resource selection because the area is used throughout the year; however, we cannot explicitly state whether this area would encompass the bison's annual population range if no peripheral fence existed. A GLMM was estimated using the lme4 package (Bates et al. 2011) for R 2.15.1 and included our covariates (described above). For categorical covariates, we selected riparian communities as the reference category for vegetation due to previous relationships between riparian communities and bison and cattle reported in the literature. East-facing slopes were selected as a reference category in relation to other cardinal directions because of perceived heat exposure. We assumed that north-facing slopes were cooler, and west- and south-facing slopes were warmer than east-facing slopes, thus influencing the selection of aspect. All variables were screened for collinearity by calculating the Pearson's correlation between variables and using $r > 0.6$ as the threshold for removing a covariate (Hosmer and Lemeshow 2000). Because analysis coefficients are relative to all other model variables,

Table 2. Chi-square comparison of bison and cattle behavior across and within species. Behavioral activities were observed from 23 May to 31 August (2010, 2011) of bison on American Prairie Reserve (APR) and Grasslands National Park (GNP) and cattle on Barnard Ranch (BR) and Weiderrick Ranch (WR). χ^2 results represent the comparison of a specified behavior against four additional behaviors. Data were pooled across years for each site and pooled across years and sites for species.

	Species comparison			Bison location comparison			Cattle location comparison		
Behavior	x^2	df	P	x^2	df	P	x^2	df	P
Grazing	1054.02	1	< 0.01	5.17	1	0.02	11.97	1	< 0.01
Standing	165.81	1	< 0.01	23.55	1	< 0.01	17.47	1	< 0.01
Bedded	1068.21	1	< 0.01	0.06	1	0.80	30.87	1	< 0.01
Moving	245.76	1	< 0.01	87.68	1	< 0.01	50.46	1	< 0.01
Other	4.39	1	0.04	0.23	1	0.63	60.58	1	< 0.01

no model selection technique was used, thus allowing a more direct comparison of covariates across location and species.

RESULTS

Behavior

Cattle and bison species differed ($P < 0.01$) in all behaviors (grazing, bedded, moving, standing, other [Table 2]) with cattle spending proportionately more time grazing and less time moving than bison (Table 3). However, the importance of landscape attributes was highlighted as both species demonstrated behavior differences across study sites. Bison behaviors differed ($P = 0.02$) between APR and GNP for grazing, standing, and moving, but not for bedded or other behaviors (Table 2). Similarly, cattle behaviors differed ($P < 0.01$) between BR and WR for all behaviors (Table 2).

Cattle spent more time at water than bison ($F_1 = 75.07$, $P < 0.01$). Cattle on BR (3.47 ± 0.27 min) and WR (4.44 ± 0.77 min) did not differ in time spent at water ($F_1 = 2.29$, $P < 0.13$). However, bison on APR (2.17 ± 0.11 min) and GNP (1.52 ± 0.09 min) differed in time spent at water ($F_1 = 19.68$, $P < 0.01$). Furthermore, the influence of temperature was dependent on the sampling location ($F_5 = 9.12$, $P < 0.01$ [Fig. 2]).

Movement

Cattle did not differ in MR across pasture units ($\beta = -0.17 \pm 0.27$ SE, $P = 0.206$), thus MR of both cattle sites were combined. In comparison, bison moved faster than cattle ($\beta = 0.62 \pm 0.08$ SE, $P < 0.01$). However, bison MR differed across sites ($\beta = -0.28 \pm 0.10$ SE, $P < 0.01$), with bison on GNP moving at a 25% faster rate than bison on APR. Thus, we compared combined cattle MR to location-specific bison MR. Following our prediction, bison exhibited faster MR on APR ($\beta = 0.41 \pm 0.11$ SE, $P < 0.01$) and GNP ($\beta = 0.69 \pm 0.0822$ SE, $P < 0.01$) than cattle. After β transformation, this equates to bison on APR and GNP moving at a 51% and 99% faster rate than cattle.

Table 3. Proportion of time of behavioral activities observed from 1 June to 31 August (2010, 2011) of bison on American Prairie Reserve (APR) and Grasslands National Park (GNP) and cattle on Barnard Ranch (BR) and Weiderrick Ranch (WR). Data were pooled across years.

	Bison		Cattle	
Behavior	APR	GNP	BR	WR
Grazing	0.26	0.28	0.45	0.49
Standing	0.15	0.18	0.24	0.20
Bedded	0.46	0.46	0.23	0.29
Moving	0.11	0.08	0.05	0.02
Other	0.02	0.02	0.02	0.00

Variance in FPT was maximized at 5 162 ± 13 (patch area = 8 368 ha) and 6 100 ± 173 (patch area = 11 690 ha) m radii for bison in APR and GNP (Fig. 3), respectively, whereas variances of cattle on BR and WR were maximized at 2 785 ± 103 (area = 2 435 ha) and 3 040 ± 254 (area = 2 901 ha) m radii, respectively (Fig. 3). Bison in GNP also showed increased variance in FPT at 9 904 ± 374 m radii; however, no large-scale response was found on APR (Fig. 3). Cattle on BR demonstrated a hierarchical response at a within-pasture-unit scale of 395 ± 53 m radii or 49 ha (Fig. 3). Cattle on WR also appeared to respond to resources at a fine scale (1 400 ± 450 m or 615 ha) in 2011; however, no response was observed in 2010.

Resource Selection

Cattle. Selection or avoidance of pasture attributes (except aspect) was similar across years and sites for cattle on BR and WR (Table 4). Cattle at both sites demonstrated strong selection for water resources and low elevations. Cattle on BR selected areas closer to roads; however, no comparison of road use by cattle on WR was possible because no major roads existed in the pasture unit. Cattle (across sites) avoided steep slopes and all vegetation types in relation to riparian communities. Cattle also demonstrated a linear response to NDVI (Fig. 4).

Bison. Resource selection by bison on APR (Table 4) was similar across years except for distance to fencing and sagebrush-steppe communities. Bison selected for sagebrush-steppe communities (relative to riparian communities) and areas farther from fencing in 2010 and avoided sagebrush-steppe communities (relative to riparian communities) and areas closer to fencing in 2011. There was no clear trend related to aspect across years. Bison selected for water sources and areas of higher elevation while avoiding roads and steeper slopes. Resource selection by bison in GNP (Table 4) within the constrained

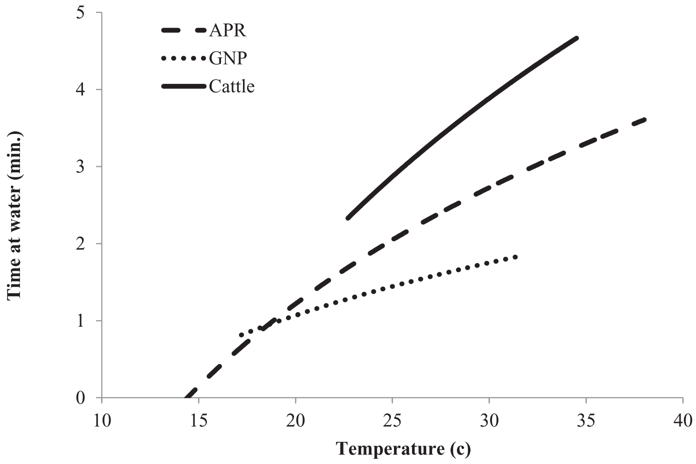

Figure 2. Influence of temperature on water use by bison on American Prairie Reserve (APR) and Grasslands National Park (GNP) and cattle on Barnard Ranch (BR) and Weiderrick Ranch (WR). Cattle did not statistically differ in time spent at water across two study locations, thus data were combined.

second order (pasture unit) and third order (summer range) demonstrated similarities to APR bison for pasture attributes across time and space, particularly in selection of water sources and areas of higher elevation. Bison in GNP avoided steep slopes and most vegetation communities relative to riparian communities, including sagebrush-steppe, upland grassland, and disturbed communities across time and space.

DISCUSSION

Interest in bison and prairie conservation has been renewed with conservationists questioning the impacts of, and differences between, domestic and native grazers at a landscape scale. Bison and cattle share a common ancestry; however, evolutionary changes that have occurred over the past 600 000 yr (MacHugh et al. 1997) lead to questions of whether the two species are, or can, serve as ecological synonyms of one another. Furthermore, complications arise when addressing these questions when bison and cattle are placed under different management strategies (Fuhlendorf et al. 2010).

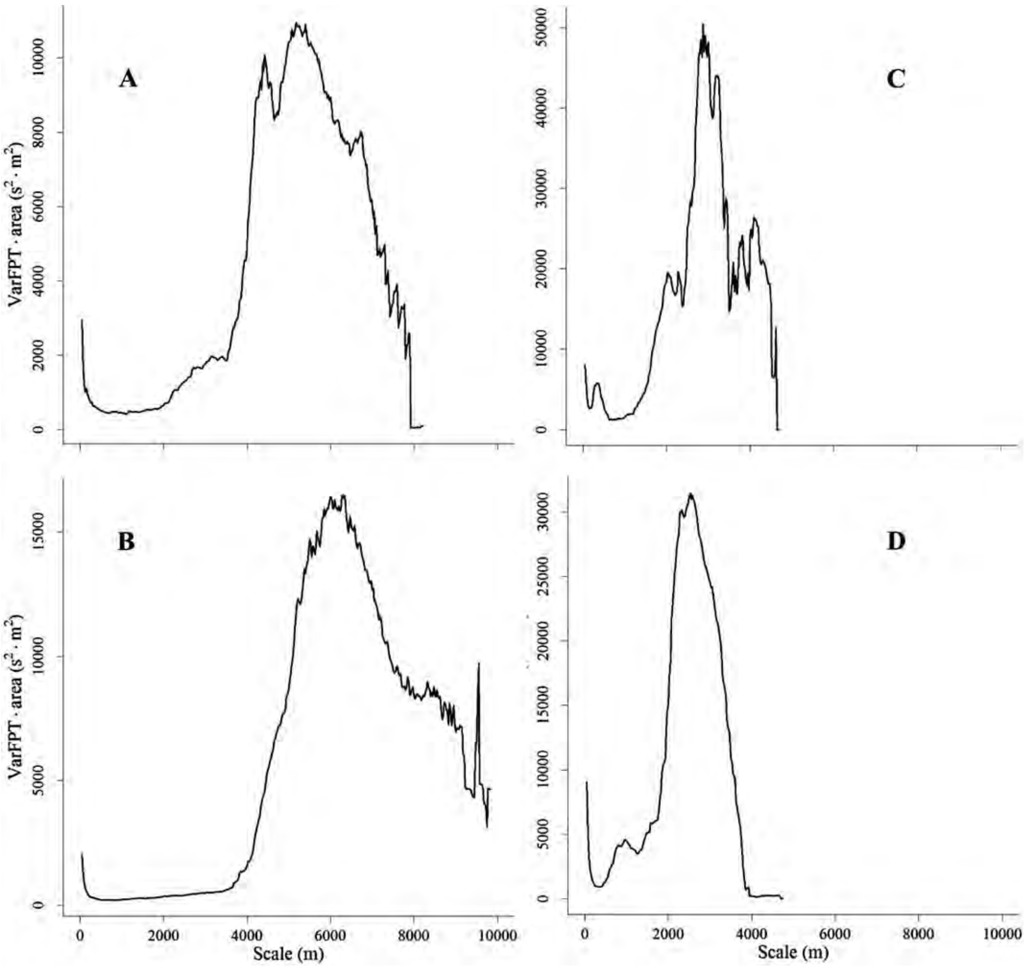

Figure 3. Examples of First Passage Time (FPT) analysis for one female bison during summer 2010 on American Prairie Reserve (**A**) and in Grasslands National Park (**B**) and for one domestic female during summer 2010 on Barnards Ranch (**C**) and on Weiderrick's Ranch (**D**). Peaks in variance of FPT (plotted up to 10 000 m) identify the spatial scale at which consumers perceive their resources. *X* axis is a measure of a circle's radius.

Table 4. Coefficient estimates from Resource Selection Functions of summer 2010 and 2011 bison use on American Prairie Reserve (APR) and Grasslands National Park (GNP). Analysis was calculated within summer range (summer) and within annual range (annual) in GNP. Coefficient values were calculated for cattle on Barnard (BR) and Weiderrick (WR) ranches. Dashes identify nonsignificant values. Variables unavailable for calculation are identified by NA. East aspect and riparian vegetation were used as reference categories. Significance at > 0.05.

Variables	Bison						Cattle			
	APR (summer)		GNP (summer)		GNP (annual)		BR		WR	
	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011
North aspect	0.2262	—	—	−0.1892	−0.3833	−0.2953	—	−0.2435	—	—
South aspect	—	—	—	—	—	−0.2882	—	0.3922	0.4299	0.2667
West aspect	0.2135	—	—	—	—	0.2608	—	0.2472	0.4456	—
Distance to fence	0.3388	—	−0.5995	—	0.1921	−0.6575	—	—	—	−0.3461
Distance to road	0.1706	0.1089	0.1383	0.112	0.6053	—	—	−1.6972	NA	NA
Distance to water	−0.4416	−0.5284	−0.1219	—	−0.4284	−0.3973	−0.5649	−0.4258	−0.9565	−1.4969
Elevation	16.0968	11.95	5.4866	6.0146	18.3053	33.146	—	—	26.8354	—
NDVI	25.6805	9.666	−17.228	—	37.6806	—	—	—	—	17.963
NDVIˆ2	−32.38	—	—	—	−43.355	55.0786	—	—	—	—
Slope	−0.1373	−0.0617	−0.0739	−0.0574	−0.0445	—	−0.0832	−0.1554	−0.0728	−0.0455
Vegetation										
Disturbed	NA	—	−1.3217	−1.2518	−1.8345	−1.5641	NA	NA	NA	NA
Eroded	0.8378	—	−0.3617	−0.5754	−1.6471	−3.4417	—	−0.9504	−1.616	14.1033
Sagebrush-steppe	0.3814	−1.073	—	−0.5006	—	−1.679	—	−0.9429	—	−0.7111
Sloped grassland	—	—	−0.3539	—	−1.679	—	—	−1.4182	—	−0.8715
Trees	NA	NA	NA	NA	—	—	−1.1957	−1.7603	NA	NA
Water bodies	—	—	NA	NA	NA	NA	NA	—	—	0.9442
Unclassified	—	—	2.3274	—	−1.1978	−5.7184	—	—	—	—
Upland grassland	NA	—	—	−0.4645	−0.2817	—	—	—	−0.743	−1.1259
Valley grassland	NA	NA	−0.3328	—	0.5064	−0.4314	NA	NA	NA	NA

Behavior

Historical accounts report that bison would graze for multiple days over distances of 80–160 km before watering, at which time they would drink heavily (Hornaday 1887a; Dary 1989). In agreement, van Vuren (1979) reported bison watering events to last 21.3 minutes in a desert landscape. However, we observed shorter watering times than those presented above. This may be due to high precipitation levels during the study, which permitted numerous short bouts of water acquisition from ephemeral water sources. The differences in water use between species, however, does provide insight into the water requirements of bison, including physiological capabilities that would permit water source removals that may lead to increased vegetation heterogeneity at a landscape scale.

Bison spent less time grazing than cattle in our study, in agreement with Plumb and Dodd (1993). However, their study reported the amount of grazing time during summer (June–October) increased from 47% to 67% for bison and from 51% to 71% for cattle. The large difference in time spent grazing by bison reported in the literature and in this study (APR=26%, GNP=28%) may be a result of different observation techniques in which group behavior (previous study) or individual behavior (this study) was recorded, thus resulting in an inability to directly compare results. However, our observations of increased grazing and decreased movements by cattle, when combined with livestock stocking levels twice that of historic bison, is compatible with the hypothesis that current range practices are resulting in homogenous grazing at a landscape scale, and thus contributing to the continued decline of prairie obligate species (Knopf 1996; Fuhlendorf et al. 2006).

Movement

Bison are effectively extinct at what are thought to be ecologically relevant scales (Freese et al. 2007). However, a definition of this spatial scale for bison has, until recently, been subjective. Lott (2002) approximated an ecological functional scale for a bison herd to be as large as 1 300 000 ha and, Sanderson et al. (2008) stated that landscapes > 200 000 ha are exceptional contributors to the ecological recovery of bison, yet little quantitative work has demonstrated the true scale that bison require.

We identified hierarchical foraging scales for cattle, indicating use of the entire pasture with movements also organized at subpasture unit scales. These smaller scales suggest that cattle perceive and move in response to landscape patches corresponding with contemporary range management guidelines that assume distances of 1.6–3.2 km from water to be of moderate forage availability and further distances considered ungrazeable by cattle (Holecheck et al. 2006). Under these guidelines, the total area surrounding a singular water resource encompasses < 813.25 ha of forage availability for cattle, lending credibility to our observations of 49 ha (BR) and 615 ha (WR) foraging patches. In comparison, bison indicated no peaks in FPT at subpasture scales. The lack of small-scale patch use by bison within APR suggests that a single bison foraging patch encompasses an area of at least the APR pasture unit (3 555 ha). These results

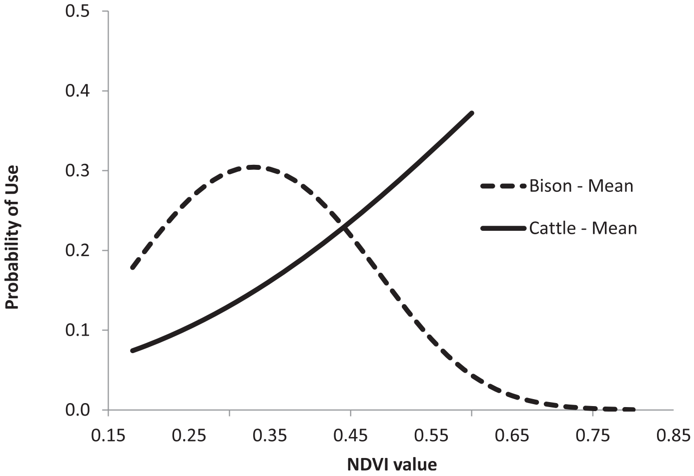

Figure 4. Averaged probability of use for intermediate green vegetation (NDVI values) for bison (at summer and annual scale) and cattle for all values (i.e., significant and nonsignificant). Selection was calculated from maximum and minimum NDVI values only and was fitted to a quadratic relationship for both species to identify whether selection was occurring for intermediate forage biomass.

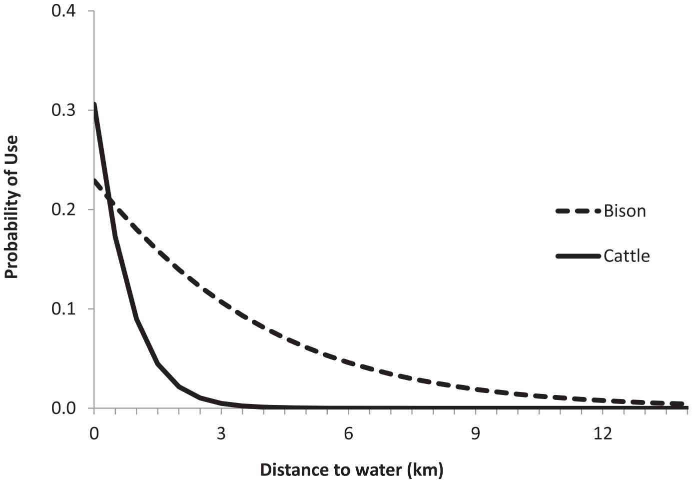

Figure 5. Probability of use for bison and cattle in relation to distance to water. Calculated using averaged values from RSF across years and locations for bison and cattle on GNP and APR.

are confirmed when we identified a bison summer foraging patch to be $\sim$11 683.94 ha in GNP where a larger pasture unit permits increased movement and landscape use. Furthermore, the largest scale identified in GNP may approximate a spatial scale used when historical bison populations are permitted to move freely across the landscape. Thus, we provide the first quantitative evidence within the Great Plains region that bison populations use larger spatial scales than cattle and may prefer larger landscapes than currently provided by managers and, as a result, would likely make different ecological contributions at such scales. In addition, FPT identifies a single resource patch, implying that multiple large patches are necessary, particularly when considering long temporal scales that bison may have used historically (i.e., overgrazing leading to landscape movements the following month, season, or year [Seton 1929]).

Previous studies using FPT to identify scales of movement by large herbivores have not examined the impact of a defined boundary (i.e., fencing) on detected scales (Frair et al. 2005; Williams et al. 2012). The fact that our FPT analyses identified scales of movement larger than the area of the fenced pasture is a result of using increasing radii around each GPS observation (i.e., the circles extend beyond the fence). We have interpreted these results as indicating that the individuals' movements are organized at a scale consistent with at least the entire pasture unit.

Resource Selection

Cattle located on the BR and WR demonstrated strong selection for riparian areas, lowlands, and water resources as predicted by other studies (van Vuren 1983; Allred et al. 2011). For bison, our results were similar to previous research in that bison selected for higher elevations (van Vuren 1979; Phillips 2000); however, we report avoidance of most vegetation communities by bison populations on APR and GNP in relation to riparian areas, a finding contrary to previous literature. These riparian areas were generally located within steep drainage areas where water availability may have existed and may have resulted in short, opportunistic watering events when bison were nearby, thus explaining the selection of these areas.

We are the first to observe selection of water resources by bison across location and spatial scale, a finding contrary to other work throughout the literature (van Vuren 1979; Phillips 2000; Babin 2009; Allred et al. 2011). As expected, we report strong selection for water by cattle with no expected use beyond 3 km from water, or ≤ 707 grazeable ha $\cdot$ water source (GH; Fig. 5). Bison selected for water, however they still used areas more than 10 km from water sources, a finding similar to McHugh (1958; Fig. 5). This is in contrast to other work and our expectations based on the abundance of ephemeral water but may simply be due to an inability to avoid water as a result of the significant precipitation during the study. Last, we confirmed the historic importance of summer temperatures on water requirements (Hornaday 1887a).

In terms of grazing, NDVI has been demonstrated as a viable metric for quantifying quality (i.e., standing nitrogen) and quantity (i.e., total biomass) in the study region (Thoma et al. 2002), thus allowing for the identification of tradeoffs between forage quality and quantity (Fryxell 1991). We report different selection relationships for forage quality/quantity by bison and cattle (Fig. 4). A quadratic relationship was fitted to each species to maintain consistency within the study; however, it is evident that cattle may be maximizing intake rate by selecting areas of higher forage biomass if maximum net energy intake occurs at intermediate biomass (where daily energy intake and forage biomass intersect [Hebblewhite et al. 2008; Fryxell 1991]). Previous work has varied across studies with cattle selecting for maximum intake (Distel et al. 1995), previously grazed areas (Silvia Cid and Brizuela 1998), higher forage quality (Bailey 1995), or areas of intersecting forage quantity and quality (Senft et al. 1985). Similar to other studies (Coppock et al. 1983; Coppedge and Shaw 1998; Bergman et al. 2001), bison selected for intermediate biomass (Fig. 4) except at the third order scale in 2011 on APR and GNP. We hypothesize these differences in 2011 are due to abundant rainfall throughout the year that may have resulted in areas of high biomass with abnormally high nutrient quality, thus relaxing the trade-off between forage quality and quantity.

IMPLICATIONS

If increased biological diversity facilitated by vegetation heterogeneity is an objective (Fuhlendorf et al. 2006) and domestic livestock are used as the dominant grazer, then the cumulative result of grazing alterations across many pasture units may reduce the impact of increased grazing periods and localized use areas by livestock, thus increasing biological diversity at a landscape scale (Fuhlendorf and Engle 2001). Potential pasture unit alterations may include changes to timing, duration, and intensity of grazing or through the use of transportable water and/or mineral sources (Ganskopp 2001; Porath et al. 2002; Bailey 2004).

If increased vegetation heterogeneity through bison grazing is an objective, then we have demonstrated that much larger pasture units may be required to facilitate bison movement, behavior, and resource use that more closely approximates historical bison populations. Although we have not quantified the pasture unit size that would permit approximations of historical use, we have provided quantitative support for the contribution of nonconstricted bison populations or populations within large pasture units to landscape vegetation heterogeneity in the Great Plains region. Due to the limited area of availability for bison in this study, we encourage similar movement analyses to be adapted to bison populations with less anthropogenic, biological, or social constrictions, thus providing additional insight into the scale of bison use across time and space. Within bison conservation areas, we have identified resources of value including variable vegetation communities that occur across upland and lowland areas. Also, we recommend testing the minimum spatial requirements of water by bison through water source reductions, thus encouraging long distance movements across the landscape that facilitate grazing heterogeneity similar to historic use (Hornaday 1887b).

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LITERATURE CITED

Allred, B. W., S. D. Fuhlendorf, and R. G. Hamilton. 2011. The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. *Ecosphere* 2(3):article 26. doi:10.1890/ES10-00152

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.

Aune, K., and C. C. Gates. 2010. Reportable or notifiable diseases. *In*: C. C. Gates, C. H. Freese, P. J. P. Gogan, and M. Kotzman [eds.]. American bison: status survey and conservation guidelines 2010. Gland, Switzerland: IUCN. p. 27– 38.

Babin, J. 2009. Nutritional determinants of space use by bison in the Great Plains [thesis]. Quebec City, Canada: University of Laval. 44 p.

Bailey, D. W. 1995. Daily selection of feeding areas by cattle in homogeneous and heterogeneous environments. *Applied Animal Behaviour Science* 45:183–200.

Bailey, D. W. 2004. Management strategies for optimal grazing distribution and use of arid rangelands. *Journal of Animal Science* 82:147–153.

Bates, D., M. Maechler, and B. Bolker. 2011. Lme4: linear mixed-effects models using S4 classes. Version 0.999375-42. Available at: http://cran.r-roject.org/web/packages/lme4/index.html. Accessed 1 November 2011.

Bennington, C. C., and W. V. Thayne. 1994. Use and misuse of mixed-model analysis of variance in ecological studies. *Ecology* 75:717–722.

Bergman, C. M., J. M. Fryxell, C. C. Gates, and D. Fortin. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology* 70:289–300.

Beyer, H. L. 2012. Geospatial modeling environment. Version 0.6.0.0. Available at: http://www.spatialecology.com/gme. Accessed 12 December 2011.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127–135.

Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. *Journal of the American Statistical Association* 88:9–25.

Calenge, C. 2006. The package adehabitat for the r software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.

Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing on seasonally burned tallgrass prairie. *Journal of Range Management* 51:258–264.

Coppock, D. L., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. *Oecologia* 56:10–15.

Dary, D. A. 1989. The buffalo book: the full saga of the American animal. Chicago, IL, USA: Swallow Press. 384 p.

Derner, J. D., W. K. Lauenroth, P. Stapp, and D. J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. *Rangeland Ecology and Management* 62:111–118.

Distel, R. A., E. A. Laca, T. C. Griggs, and M. W. Demment. 1995. Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. *Applied Animal Behaviour Science* 45:11–21.

Fauchald, P., and T. Tveraa. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288.

Forrest, S. C., H. Strand, W. H. Haskins, C. Freese, J. Proctor, and E. Dinerstein. 2004. Ocean of grass: a conservation assessment for the Northern Great Plains. Bozeman, MT, USA: Northern Plains Conservation Network and Northern Great Plains Ecoregion. 191 p.

Fortin, D., J. M. Fryxell, L. O'Brodovich, and D. Frandsen. 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. *Oecologia* 134:219–227.

Fox, J. 2005. The r commander: a basic statistics graphical user interface for r. *Journal of Statistical Software* 14:1–41.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology* 20:273–287.

Freese, C. H., K. E. Aune, D. P. Boyd, J. N. Derr, S. C. Forrest, C. C. Gates, P. J. P. Gogan, S. M. Grassel, N. D. Halbert, K. Kunkel, and K. H. Redford. 2007. Second chance for the plains bison. *Biological Conservation* 136:175–184.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 131:781–798.

Fuhlendorf, S. D., B. W. Allred, and R. G. Hamilton. 2010. Bison as keystone herbivores on the Great Plains: can cattle serve as proxy for evolutionary grazing patterns. Bronx, NY, USA: American Bison Society Working Paper No. 4. 48 p.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51:625–632.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie, Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* 16:1706–1716.

Ganskopp, D. 2001. Manipulating cattle distribution with salt and water in large arid-land pastures: a GPS/GIS assessment. *Applied Animal Behavior Science* 73:251–262.

GATES, C. C., C. H. FREESE, P. J. P. GOGAN, AND M. KOTZMAN. 2010. American bison: status survey and conservation guidelines 2010. Gland, Switzerland: IUCN. 154 p.

HALBERT, N. D., AND J. N. DERR. 2007. A comprehensive evaluation of cattle introgression into US federal bison herds. *Journal of Heredity* 98:1–12.

HEBBLEWHITE, M., E. MERRILL, AND G. MCDERMID. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78:141–166.

HOLECHECK, J. L., R. D. PIEPER, AND C. H. HERBEL. 2006. Range management principles and practices. 6th ed. Upper Saddle River, NJ, USA: Prentice Hall. 456 p.

HORNADAY, W. T. 1887a. The extermination of the American bison with a sketch of its discovery and life history. p. 418–420. Washington, DC, USA: Report of the U.S. National Museum, 1887, part 2. 548 p.

HORNADAY, W. T. 1887b. The extermination of the American bison with a sketch of its discovery and life history. p. 377. Washington, DC, USA: Report of the U.S. National Museum, 1887, part 2. 548 p.

HOSMER, D. W., AND S. LEMESHOW. 2000. Applied logistic regression. 2nd ed. New York, NY, USA: John Wiley & Sons. 392 p.

HUETE, A., K. DIDAN, T. MIURA, E. P. RODRIGUEZ, X. GAO, AND L. G. FERREIRA. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83:195–213.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.

KNAPP, A. K., J. M. BLAIR, J. M. BRIGGS, S. L. COLLINS, D. C. HARTNETT, L. C. JOHNSON, AND E. G. TOWNE. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* 49:39–50.

KNOPF, F. L. 1996. Prairie legacies—birds. *In:* F. B. Samson and F. L. Knopf [EDS.]. Prairie conservation: preserving North America's most endangered ecosystem. Washington, DC, USA: Island Press. p. 135–148.

KOMERS, P. E., F. MESSIER, AND C. C. GATES. 1992. Search or relax: the case of bachelor wood bison. *Behavioral Ecology and Sociobiology* 31:195–203.

LOTT, D. F. 2002. American bison: a natural history. Los Angeles, CA, USA: University of California Press. 229 p.

MACHUGH, D. E., M. D. SHRIVER, R. T. LOFTUS, P. CUNNINGHAM, AND D. G. BRADLEY. 1997. Microsatellite DNA variation and the evolution, domestication and phylogeography of Taurine and Zebu cattle (*Bos Taurus* and *Bos indicus*). *Genetics* 146:1071–1086.

MANLY, B. F. L., L. L. MCDONALD, D. L. THOMAS, T. L. MCDONALD, AND W. P. ERICKSON. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd ed. Kluwer Norwell, MA, USA: Academic Publishers. 240 p.

MCHUGH, T. 1958. Social behavior of the American buffalo (*Bison bison bison*). *Zoologica* 43: 1–40.

MORALES, J. M., D. FORTIN, J. L. FRAIR, AND E. H. MERRILL. 2005. Adaptive models for large herbivore movements in heterogeneous landscapes. *Landscape Ecology* 20:301–316.

PEDEN, D. G., G. M. VAN DYNE, R. W. RICE, AND R. M HANSEN. 1974. The trophic ecology of Bison bison L. on shortgrass plains. *Journal of Applied Ecology* 11:489–497.

PHILLIPS, L. B. 2000. GIS modeling of bison habitat in southwestern Montana: a study in ranch management and conservation [thesis]. Bozeman, MT, USA: Montana State University. 87 p.

PLUMB, G. E., AND J. L. DODD. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecological Applications* 3:631–643.

PORATH, M. L., P. A. MOMONT, T. DELCURTO, N. R. RIMBEY, J. A. TANAKA, AND M. MCINNIS. 2002. Offstream water and trace mineral salt as management strategies for improved cattle distribution. *Journal of Animal Science* 80:346–356.

POWELL, F. L. A. 2006. Effects of preseribed burns and bison (Bos bison) grazing on breeding bird abundances in tallgrass prairie. *The Auk* 123:183–197.

SANDERSON, E. W., K. H. REDFORD, B. WEBER, K. AUNE, D. BALDES, J. BERGER, D. CARTER, C. CURTIN, J. CURTIN, J. DERR, S. DOBROTT, E. FEARN, C. FLEENER, S. FORREST, C. GERLACH, C. C. GATES, J. E. GROSS, P. GOGAN, S. GRASSEL, J. A. HILTY, M. JENSEN, K. KUNKEL. D. LAMMERS, R. LIST, K. MINKOWSKI, T. OLSON, C. PAGUE, P. B. ROBERTSON, AND B. STEPHENSON. 2008. The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. *Conservation Biology* 22:252–266.

SENFT, R. L., L. R. RITTENHOUSE, AND R. G. WOODMANSEE. 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. *Journal of Range Management* 38:82–87.

SETON, E. T. 1929. Lives of game animals. 4 vols. Garden City, NY, USA: Doubleday, Doran & Co. 2640 p.

Silvia Cid, M., and M. A. Brizuela. 1998. Heterogeneity in tall fescue pastures created and sustained by cattle grazing. *Journal of Range Management* 51:644–649.

THOMA, D. P., D. W. BAILEY, D. S. LONG, G. A. NIELSEN, M. P. HENRY, M. C. BRENEMAN, AND C. MONTAGNE. 2002. Short-term monitoring of rangeland forage conditions with AVHRR imagery. *Journal of Range Management* 55:383–389.

TOWNE, E. G., D. C. HARTNETT, AND R. C. COCHRAN. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecological Applications* 15:1550–1559.

TUCKER, C. J., AND P. J. SELLERS. 1986. Satellite remote sensing for primary production. *International Journal of Remote Sensing* 7:1395–1416.

TURCHIN, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sunderland, MA, USA: Sinauer. 396 p.

VAN VUREN, D. 1979. Ecology and behavior of bison in the Henry Mountains, Utah [thesis]. Corvallis, OR, USA: Oregon State University. 47 p.

VAN VUREN, D. 1983. Group dynamics and summer home range of bison in southern Utah. *Journal of Mammalogy* 64:329–332.

VENABLES, W. N., AND B. D. RIPLEY. 2002. Modern applied statistics with S. 4th ed. New York, NY, USA: Springer. 512 p.

WILLIAMS, D. M., A. C. DECHEN QUINN, AND W. F. PORTER. 2012. Landscape effects on scales of movement by white-tailed deer in agricultural-forest matrix. *Landscape Ecology* 27:45–57.

A Critical Review of Assumptions About the Prairie Dog as a Keystone Species

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ABSTRACT / Prairie dogs (*Cynomys* spp.) have been labeled as keystone species because of their influence on biological diversity and ecosystem function. However, the validity of several assumptions used to support keystone status is questionable. We review the strength of the evidence and the magnitude of the prairie dog's effects on ecosystem structure and function. We use this review to reevaluate the keystone role for prairie dogs. Our goal is to encourage sound management of the prairie dog ecosystem by improving the ecological foundation of their keystone status.

Our review confirms that prairie dogs affect a number of ecosystem-level functions but that their influence on prairie vertebrates may be less than previously suggested. Species richness and abundance patterns were variable among plants, mammals, and birds and were not consistently higher on prairie dog colonies compared to uncolonized areas. In addition, only nine of the 208 species listed in the literature as observed on or near prairie dogs colonies had quantitative evidence of dependence on prairie dogs. Abundance data indicated opportunistic use of colonies for an additional 20 species. A total of 117 species may have some relationship with prairie dogs, but we lacked sufficient data to evaluate the strength of this relationship. The remaining 62 species may be accidental or alien to the system.

Despite our conclusion that some prairie dog functions may be smaller than previously assumed, collectively these functions are quite large compared to other herbivores in the system. We suggest that prairie dogs also provide some unique functions not duplicated by any other species and that continued decline of prairie dogs may lead to a substantial erosion of biological diversity and landscape heterogeneity across prairie and shrub-steppe landscapes. Thus, we concur that keystone status for prairie dogs is appropriate and may aid conservation efforts that help protect species dependent on prairie dogs and support other important ecosystem functions.

The much maligned prairie dog has been the target of widespread eradication campaigns over the past century, largely as a consequence of their reputation as range and agricultural pests (Clark 1989). Sylvatic plague and habitat loss have also contributed to the estimated 98% population decline in prairie dog numbers (Marsh 1984, Anderson and others 1986, Miller and others 1990, Cully 1993). Particularly severe reductions of the Utah prairie dog (*Cynomys parvidens*) have prompted its listing as a federally threatened species.

Where prairie dogs still persist, they conspicuously alter prairie landscapes and provide foraging, shelter, and nesting habitat for a diverse array of species. Prairie dogs serve as prey for a number of predators including black-footed ferrets and prairie rattlesnakes (see Appendix 1 for scientific names). Their burrows provide nest sites and shelter for vertebrates such as tiger salamanders and burrowing owls, as well as for invertebrates. Prairie dogs alter plant species composition and vegetation structure (Whicker and Detling 1988), creating open habitats. They also can affect ecosystem processes such as disturbance and nutrient cycling rates (Whicker and Detling 1988).

Prairie dogs have been labeled a keystone species based on the assumption that they have a pronounced effect on biological diversity in prairie systems (Reading and others 1989, Miller and others 1994, Benedict and others 1996, Roemer and Forrest 1996, Weltzin and others 1997a, Wuerthner 1997). It has been argued that if we save prairie dogs, we save a key component of the prairie ecosystem that includes declining grassland species considered dependent upon prairie dog colonies for survival (Miller and others 1990, 1994). Thus, prairie dogs have been targeted as a conservation

KEY WORDS: Prairie dogs; *Cynomys* spp.; Keystone species; Ecosystem functions; Biological diversity

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priority. Indeed, the black-tailed prairie dog (*C. ludovicianus*) was recently petitioned to receive candidate species status under the Endangered Species Act, based in part on its role in supporting numerous dependent species (Biodiversity Legal Foundation and Sharps 1994). This petition was denied, in part, because the petitioners' conclusions about the purported keystone role of prairie dogs in the prairie system were deemed equivocal (Gill 1995).

Prairie dogs clearly have an important role in grassland systems. It is our premise, however, that the magnitude of the prairie dog's role has been overstated in the literature. Here we review the evidence supporting the following assumptions that have been cited as evidence of their keystone role: (1) prairie dogs regulate ecosystems (Hansen and Gold 1977, O'Meilia and others 1982, Agnew and others 1986, Miller and others 1990); (2) passerine, small mammal, and predator abundance is higher at colonies (O'Meilia and others 1982, Clark and others 1982, Agnew and others 1986, Krueger 1986, Sharps and Uresk 1990, Reading and others 1989, Miller and others 1990, 1994); (3) species richness and diversity is higher at colonies (Hansen and Gold 1977, O'Meilia and others 1982, Agnew and other 1986, Clark and others 1982, Reading and others 1989, Sharps and Uresk 1990, Miller and others 1990, 1994); and (4) over 200 vertebrate species are associated with prairie dog colonies (Campbell and Clark 1981, Clark and others 1982, Reading and others 1989, Sharps and Uresk 1990, Biodiversity Legal Foundation and Sharps 1994, Miller and others 1990, 1994). We reviewed over 200 references on prairie dogs and associated taxa dating back as early as 1902. We focus on black-tailed prairie dogs because they are the most extensively studied and the most widely distributed of the prairie dog species, but also include evidence for Mexican prairie dog (*C. mexicanus*), white-tailed prairie dog (*C. leucurus*), Utah prairie dog, and Gunnison's prairie dog (*C. gunnisoni*).

Based on the strength of existing evidence, we then reevaluate whether prairie dogs function as a keystone species. We use Paine's (1969) original definition of keystone species, which reflects species whose activities greatly influence the composition, integrity, and functioning of communities. We also use a more recent definition proposed by Power and others (1996), who define a keystone species as one whose overall impact on a community is large, as well as disproportionately large relative to its abundance. We conclude that although some aspects of their role have been overstated in the literature, the available evidence clearly indicates that prairie dogs function as a keystone species. We also suggest that only well-documented ecological functions of prairie dogs should be the basis for management decisions.

Review of the Prairie Dog's Role

Ecosystem Regulation

The disturbance caused by grazing and burrowing activities of prairie dogs affects a number of ecosystem-level processes (Whicker and Detling 1988). Prairie dog grazing affects vegetation structure by decreasing vegetation height and cover and altering plant species composition (Coppock and others 1983a, Brizuela and others 1986, Cid and others 1989, Cincotta and others 1989, Weltzin and others 1997a,b). Prairie dog burrowing and grazing can also affect the rates of nitrogen cycling and lead to increased nitrogen uptake by plants (Holland and Detling 1990), which may account for the preferential grazing of prairie dog colonies by pronghorn, elk and bison (Coppock and others 1983b, Krueger 1986, Wydeven and Dahlgren 1985). Below ground, prairie dogs increase soil mixing and affect rates of energy and material flows (Ingham and Detling 1984). Across the landscape, variation in colony density and duration of occupancy can lead to a shifting mosaic of patches that differ in vegetation structure, composition, and quality (e.g., nutrient availability) within and among patches (Bonham and Lerwick 1976, Archer and others 1987). Cumulatively, prairie dog activities influence patch dynamics and contribute to overall landscape heterogeneity.

Superimposed over the disturbance caused by prairie dogs are the impacts of fire and climatic variability. These processes generally operate at spatial scales much greater than the scale of individual prairie dog colonies, although human activities have decreased the scale of both fire and prairie dog disturbance regimes. The patch-level disturbance created by prairie dogs interacts with these large-scale disturbances, altering their effects on landscape structure and dynamics (Coppock and Detling 1986, Weltzin and others 1997a). For example, prairie dog colonies may serve as fire breaks and may also magnify the effects of cyclical and seasonal drought. Higher than average rainfall may either enhance or diminish the effects of prairie dog disturbance. Historically, bison were also an important agent of disturbance across the Great Plains and may have influenced the dispersal and distribution of prairie dogs and may have selectively grazed prairie dog colonies (Coppock and others 1983b, Krueger 1986, Wydeven and Dahlgren 1985).

Collectively, these direct and indirect impacts of prairie dog grazing and burrowing have a pronounced effect on ecosystem processes and patterns, even though prairie dog numbers are only a fraction of historic levels. Considering that the historic range of prairie dogs may well have covered over 40 million ha (Anderson and others 1986), their impact on landscape structure and dynamics must have been dramatic.

Abundance Patterns

It is frequently cited that the overall abundance of birds, small mammals, and terrestrial predators is higher on colonies (O'Meilia and others 1981, Clark and others 1982, Agnew and others 1986, Reading and others 1989, Miller and others 1990, 1994, Sharps and Uresk 1990). However, several details have been omitted that bear on the interpretation of these patterns. The higher abundance (total individuals) of small mammals and passerines on colonies relative to adjacent areas (O'Meilia and others 1982, Agnew and others 1986, Mellink and Madrigal 1993, Barko 1996) can be accounted for solely by the abundance patterns of deer mice, grasshopper mice, and horned larks. Higher terrestrial predator abundance is based on the statement that "dog towns had 5.7 times the frequency of predators (coyotes and badgers) as off-town areas" (Krueger 1986); however, the validity and generality of this pattern cannot be evaluated because no information on methods and analysis were provided in this paper.

Species Richness Patterns

Keystone species commonly affect community structure by increasing species richness (Mills and others 1993). Although it is widely stated that prairie dogs can increase species richness (Hansen and Gold 1977, Clark and others 1982, O'Meilia and others 1982, Reading and others 1989, Miller and others 1990, 1994), prairie dogs do not appear to consistently increase species richness and may sometimes decrease richness at the scale of individual colonies. Agnew and others (1986) found that out of a total of 39 bird species, 36 species occurred on colonies compared to 29 species off colonies, a pattern frequently used to assert the keystone role of prairie dogs (Reading and others 1989, Miller and others 1990, 1994). Although the entire list of 36 species observed on colonies was not provided, their results indicate that at least seven of these species were from a species pool that included exotics (rock dove, European starling, house sparrow) or waterbirds (mallard, northern pintail, blue-winged teal, sora, yellow-headed blackbird). It is unlikely these species evolved a strong relationship with prairie dogs. In a similar study, 30 species were found on colonies compared to 27 species in adjacent uncolonized areas (Barko 1996). Thus, the available evidence indicates that there may be only a minimal contribution to colony-scale biological diversity accounted for by an increase in avian species richness on colonies.

For small mammals, species richness may actually be lower on colonies compared to nearby uncolonized areas (O'Meilia and others 1982, Agnew and others 1986, Mellink and Madrigal 1993). In addition, several species of rodents observed in uncolonized areas are completely absent from colonies (O'Meilia and others 1982, Agnew and others 1986, Mellink and Madrigal 1993). This pattern often has been overlooked in summaries of the prairie dog's role.

Plant species richness is probably related to the degree of prairie dog disturbance. Intermediate disturbance levels have the greatest floral species richness, although this pattern varies somewhat among forbs, grasses, and shrubs (Whicker and Detling 1988). Plant species richness can also vary within colonies as a function of colony age (Whicker and Detling 1988). In addition, species richness patterns may vary across seasons, vegetation types (e.g., shortgrass prairie vs shrub-steppe), and prairie dog species (Weltzin and others 1997b).

This confusing array of richness patterns indicates that using these patterns to characterize the role of prairie dogs is problematic. Species richness at the scale of colonies provides little information about how prairie dogs influence the integrity of the community. This is better addressed by comparing species composition, which can differ among areas with and without prairie dogs. Many plant and animal species reach their highest densities on colonies. For example, the reduction of little bluestem (*Andropogon scoparius*) on black-tailed colonies may allow annual forbs, such as prairie dogweed (*Dyssodia papposa*) to increase in abundance relative to undisturbed prairie, where they are quite rare (Coppock and others 1983a). In mesquite grasslands, historic populations of black-tailed prairie dogs, in conjunction with other herbivores associated with colonies, may have prevented woody species such as mesquite (*Prosopis* spp.) from attaining dominance (Weltzin and others 1997a). Thus, changes in species composition resulting from prairie dogs can increase species richness, but at scales much larger than previously studied.

Dependence of Vertebrates on Prairie Dog Colonies

Criteria for establishing dependence. Another way to evaluate the influence of prairie dogs on the integrity of the system is to quantify the degree to which species depend on prairie dogs. We defined dependent species as those species whose fitness is increased by the

Table 1. Strength of dependence/association of 208 vertebrate species found in proximity to prairie dog towns

Strength of association	Definition	If prairie dogs go extinct	Possible examples
Dependent species			
Obligate	Almost totally dependent upon prairie dogs for survival	Species goes extinct	Black-footed ferret
Facultative			
Strong	Use one or more features of prairie dog towns that have limited availability off towns	Decrease in local and regional abundance	Burrowing owl, mountain plover
Weak	Use features of prairie dog towns that are also abundant off towns, or use of towns varies in space or time	Abundance may decrease locally if alternative habitats limiting	Ferruginous hawk, horned lark
Associated species			
Opportunistic	Species more generally associated with prairie grasslands; occur on prairie dog towns, but tend to be more abundant off towns	Little or no change in abundance; may increase if undisturbed habitat preferred	Western diamondback rattlesnake, western meadowlark, pronghorn
Accidental	Do not use features of towns, but are seen on, or near, towns due to habitat features that occur in proximity to towns	No change likely	Yellow warbler, white pelican, ladder-backed woodpecker
Alien	Exotic or domestic animals	No change likely	Domestic cattle, house sparrow, Norway rat

presence of prairie dogs, which included both obligate (require prairie dogs for survival) and facultative species (use features of prairie dog colonies that have limited availability elsewhere; Table 1). We compiled a list of 208 vertebrate species that have been cited as associated with prairie dogs (Appendix 1; references in Table 2). Prairie dog associates have been minimally defined as those species seen on, near, or flying over prairie dog colonies and does not reflect use of prairie dog colonies. Consequently, this list includes species that range in association from obligate species to species associated with habitat features (e.g., wetlands, reservoirs, trees) located on or near colonies that are not a consequence of prairie dog activities (Table 1). We developed four criteria to determine which of the 208 species listed as prairie dog associates are truly dependent upon prairie dogs:

1. *Abundance of species is higher on prairie dog colonies than comparable areas without prairie dogs.* In general, a greater disparity in abundance indicates a greater degree of dependence. However, because this criterion is based on correlational patterns, it provides only weak evidence of dependence.

2. *Species use features of prairie dog towns, which are a direct consequence of prairie dog activities or presence, at greater frequencies than similar features off colonies.* This criterion helps to quantify the degree of specialization on features of prairie dog colonies. For instance, burrowing owls may use prairie dog burrows at a greater frequency than the burrows of other species.

3. *Survivorship or reproductive success is lower off prairie dog colonies than on colonies.* Thus, colonies may serve as sources of recruitment, whereas alternative habitats may constitute ecological sinks that require continued immigration to maintain populations. For example, although mountain plovers and horned larks sometimes nest on agricultural land, agricultural practices may reduce nest success (Hurley and Franks 1976, Knopf and Rupert 1998).

4. *Populations of dependent species decline if prairie dog populations decline.* Declines in strongly dependent species should occur both locally and regionally if prairie dogs are extirpated. Species only marginally dependent on colonies might decline locally, but not regionally, if availability of alternative habitats is sufficient to support populations elsewhere across their range. For example, in several areas in Colorado and New Mexico, wintering and migrating ferruginous hawk numbers declined locally following a crash in prairie dog populations as a result of a sylvatic plague (*Yersinisia pestis*) epizootic (Jones 1989, Cully 1991). Evidence of meeting this criterion, particularly in combination with decreased fitness off colonies, is the most compelling support for dependence.

Documenting dependence on prairie dogs is rather difficult. Because dependence can vary in space and time, scale of analysis is crucial. For example, horned larks may be more abundant on colonies compared to nearby undisturbed areas (Agnew and others 1986, Barko 1996), but may reach numbers comparable to

Table 2. Review of studies providing lists of species associated with prairie dog colonies

Authors	Location	No. of colonies	Prairie dog species[a]	On/off colonies	Quantified methods	Results[b]	No. spp/taxa Herps	Birds	Mammals
Koford 1958	ND, SD, WY, CO	>4	BT	On	No	SL	2	6	14
Tyler 1968	OK	280	BT	On	No	SL,[c] SA, HU, LR	17	56	16
Agnew and others 1986	MT	3	BT	On/off	Yes[d,e]	SL,[f] SR, SA[f]		36	4
Campbell and Clark 1981	WY	46	BT	On	No	SL	9	33	22
Clark and others 1982	NM, CO, WY	47	BT, WT, GU	On	Yes[g]	SL	26	51	30
O'Meilia and others 1982	OK	6	BT	On/off[h]	Yes[e]	SL, SR, SA			6
Mellink and Madrigal 1993	Mexico	1	MX	On/off[i]	Yes[e]	SL, SR, SA			5
Reading and others 1989	MT	16	BT	On	Yes[g]	SL, LR	1	70	12
Sharps and Uresk 1990	SD	?	BT	On	No	SL, LR	10	88	36
Barko 1996	OK	5	BT	On/off	Yes[d,g]	SL,[c] SR, SA		32	

[a] BT = black-tailed, WT = white-tailed, GU = Gunnison's, MX = Mexican.

[b] SL = species lists, SR = compared species richness on and off colonies, SA = species abundance, HU = information on habitat use, LR = lists includes additional species from literature review.

[c] Excluded species observed that did not use colony features.

[d] Number of visits/colony unclear.

[e] Statistical analysis of abundance patterns provided.

[f] Only partial lists of bird species provided.

[g] Sampling effort variable per colony.

[h] Experimental release of prairie dogs.

[i] Compared occupied to abandoned.

that found on colonies on otherwise disturbed prairie habitat or outside the prairie dogs' range (Hurley and Franks 1976). Taken individually, each criterion cannot sufficiently rule out alternative explanations for correlational patterns consistent with dependence. For example, secretive species may appear more abundant on colonies than in adjacent taller vegetation merely because of detection differences. In addition, failure to meet a specific criterion could result from lack of data, because not all criteria are required for dependence, or because a species is truly not dependent on prairie dogs. Thus, nondependent species may sometimes appear to meet a single criterion or dependent species may not satisfy every criteria. Convincing evidence of dependence on prairie dogs will generally require meeting more than one criterion but not necessarily all four.

Results of dependence analysis. We found that few of these criteria were met by most presumed prairie dog associates. Only nine vertebrate species had data documenting at least one of the four criteria (Table 3). Furthermore, data addressing fitness (criterion 3) was available for only two species. Other vertebrate species (e.g., badger, tiger salamander, prairie rattlesnake) are often assumed to be dependent on prairie dogs, but there are currently no published data to support this. Further work is clearly needed to confirm, or rule out, dependence for many of these candidate dependent species and to determine if other species meet any of the four dependence criteria.

Species ranged in their degree of association from obligate to opportunistic use of colonies (Table 1). Only one species, the black-footed ferret, is truly an obligate. This species is near extinction primarily due to a range-wide decimation of the prairie dog ecosystem, in conjunction with secondary poisonings and susceptibility to distemper and plague (Clark 1989). Mountain plovers and burrowing owls may be strongly facultative species because they apparently have suffered population declines within the prairie dog's range following declines in prairie dogs. These three species had the strongest evidence for dependence.

The remaining six candidate dependent species had weaker evidence of dependence and each met only one

Table 3. Species listed as prairie dog associates that meet one or more criteria for dependence

Species	Black-footed ferret[a]	Burrowing owl[b]	Mountain plover[c]	Ferruginous hawk[d]	Golden eagle[e]	Swift fox[f]	Horned lark[g]	Deer mouse[g]	Grasshopper mouse[h]
Criterion 1 Abundance higher on colonies	*[i]	*	*				*	*	*
Criterion 2 Greater use of colonies	*	*	*						
Criterion 3 Fitness higher on colonies	*		*						
Criterion 4 Population declines with prairie dog decline	*	*	*	*	*	*			

[a] Anderson and others 1986, Biggins and Godbey 1995, Biggins and others 1985, 1993, Clark and others 1985, Forrest and others 1985, Hilman and Linder 1973, Sheets and others 1972.

[b] Agnew and others 1986, Barko 1996, Butts and Lewis 1982, Desmond and Savidge 1996, Hughes 1993, Martin 1973, Zarn 1974.

[c] Barko 1996, Graul and Webster 1976, Knopf 1996, Knopf and Rupert 1998, Knowles and Knowles 1984, Knowles and others 1982, Olson 1985, Olson and Edge 1985, Olson-Edge and Edge 1987.

[d] Blair and Schitoskey 1982, Cully 1991, Gilmer and Stewart 1983, Houston and Bechard 1984, Howard and Wolfe 1976, Jones 1989, Lokemoen and Duebbert 1976, MacLaren and others 1988, Steenhoff and Kochert 1985, Wakely 1978, Woffinden and Murphy 1977, 1989.

[e] Cully 1991, Jones 1989.

[f] Hilman and Sharps 1978, Hines and Case 1991, Sharps 1989, Uresk and Sharps 1986, Zumbaugh and Choate 1985.

[g] Agnew and others 1986, Barko 1996, Cutter 1958, Kilgore 1969.

[h] Agnew and others 1986, O'Meilia and others 1982.

[i] Denotes criteria supported by data.

of the four criteria (Table 3). These species would probably decline locally following a decline in prairie dogs if alternative prey or habitat were unavailable (i.e., weakly facultative; Table 1). Examples include ferruginous hawks, golden eagles, and swift foxes, which are generalist predators that likely feed on prairie dogs in an opportunistic manner, but may specialize locally on prairie dogs when alternative prey sources are scarce. Evidence of dependence by ferruginous hawks and golden eagles is indicated by local declines during migration and on wintering grounds in New Mexico and Colorado following prairie dog population declines (Jones 1989, Cully 1991). In addition, wintering ferruginous hawks in Colorado typically have higher abundances on prairie dog colonies than areas without prairie dogs (Kotliar, unpublished data). A decline in swift foxes in South Dakota was also observed following declines in prairie dogs (Sharps 1989). South Dakota is the only area where data indicate that prairie dogs comprise a sizable proportion of the swift fox diet (Hillman and Sharps 1978, Uresk and Sharps 1986), which is otherwise usually dominated by nocturnal rodents (Kilgore 1969). The other three weakly facultative species (horned lark, deer mouse, and grasshopper mouse) are generalists that use open areas created by prairie dog activities. Horned lark abundance was one to two orders of magnitude higher on prairie dog colonies compared with uncolonized grasslands (Agnew and others 1986). Deer mice and grasshopper mice, although relatively abundant off colonies, were observed at densities three to four times higher on prairie dog colonies compared to uncolonized grassland (O'Meilia and others 1982, Agnew and others 1986). The degree to which any of these species would actually decline or simply move elsewhere if prairie dogs decline, however, is unclear and depends on whether prey, burrows, or open habitat is limiting. However, the limited data suggest that prairie dogs may influence the distribution patterns of these six species across the landscape.

What about the remaining 199 associated species? Abundance data for criterion 1 were only available for 20 species: five species reached slightly higher abundance levels on colonies, five species had similar abundance levels on and off colonies or had mixed patterns, and ten species had higher abundance levels off colonies (Appendix 1). This indicates that these 20 species at least occasionally occur on colonies, but probably do not prefer colonies, and may even prefer undisturbed grasslands (e.g., grasshopper sparrow).

An additional 117 species lacked abundance data on and off colonies, but their life history information indicated they could potentially use colony attributes. This included species that are often presumed to be prairie dog dependents (e.g., tiger salamander, prairie rattlesnake, badger), but which lack data to document dependence. It also included species such as western harvest mice that may actually prefer undisturbed grasslands. Fifteen species use ephemeral pools that sometimes develop on colonies. Prairie dogs may not be responsible for the rare occurrence of these shallow ponds, but their activities keep them relatively free of vegetation, a condition that may be preferred by amphibians and shorebirds that use these pools.

Of the remaining 62 species, 10 are domestic and exotic species (Table 1). Most of the remaining 52 species are waterbirds, more commonly associated with deep water (e.g., waterfowl, pelicans), that may have been observed flying over, or near, a prairie dog colony, but not actually using the colony. Although we cannot rule out the possibility that these species were using the colonies, we suggest that based on habitat affinities, many, if not most, of these 52 species were probably accidental. Because lists of species associated with prairie dog colonies have been used to justify conservation of prairie dogs, caution should be used when including potentially accidental and exotic species in lists of prairie dog associates.

Our evaluation of dependence highlights the considerable range in strength of association with prairie dogs for the 208 species. Life history information and expert review of species lists suggests that many purported associated species have a weak relationship to prairie dogs at best. We also stress that for most species, relationships to prairie dogs cannot be determined from available data. Even in studies in which data were available, sample sizes and geographic coverage were often small (Table 2). Considering that association with prairie dogs probably varies across habitats and species of prairie dog, extrapolation outside the geographic coverage of one particular study is tenuous. Further research is clearly needed to clarify the relationship of most of the 208 species to prairie dogs.

In summary, our review of both species richness patterns and assessment of strength of association suggests that the prairie dog's influence on vertebrate species richness may be lower than frequently asserted. Nevertheless, prairie dogs substantially contribute to biological diversity across their range because prairie dog colonies support a different composition of species than uncolonized areas (O'Meilia and others 1982, Agnew and others 1986, Mellink and Madrigal 1993). In addition, potentially dependent species such as black-footed ferrets, mountain plovers, burrowing owls, ferruginous hawks, and swift foxes have suffered population declines, and many either have, or are under consideration for, special protection under the Endangered Species Act (Samson and Knopf 1994). Because the long-term viability of declining dependent species may be compromised should prairie dogs continue to decline, management for prairie dogs will clearly benefit these species that are at risk.

Are Prairie Dogs a Keystone Species?

Paine's Keystone Species

To reevaluate the keystone role of prairie dogs, we first assess whether our revised prairie dog role is consistent with Paine's original concept of a keystone species whose "activities greatly modified species composition and physical appearance" and determined "the integrity of the community and its unaltered persistence" (Paine 1969). Our review indicates that nine vertebrate species may decline or disappear at a local scale, and in several cases at a landscape scale, if prairie dogs are eliminated. The black-footed ferret is apparently so specialized on prairie dogs that it does not persist where prairie dogs are eliminated. In addition, the continued reduction of prairie dog populations could hasten the demise of mountain plovers and burrowing owls, or decrease the abundance and distribution of the ferruginous hawk, golden eagle, swift fox, horned lark, grasshopper mouse, and deer mouse, diminishing biological diversity across prairie landscapes. Thus, it is not necessary to believe that prairie dogs have 208 associated species to conclude that they affect community integrity.

The disturbance activities of prairie dogs are akin to the disturbance role of the starfish (*Pisaster*) in the rocky intertidal that Paine used as a model of a keystone predator (Paine 1966, 1969). This disturbance role affects both species composition and ecosystem functions. Prairie dogs are not the only agents of disturbance in the Great Plains, but the scale at which they operate is unique. Prairie dogs aggregate into colonies that are sometimes quite dense and large, often persisting at a site over several decades. Their sedentary and colonial behavior tends to concentrate disturbance to a greater degree than the more dispersed and shorter duration disturbances caused by the actions of other

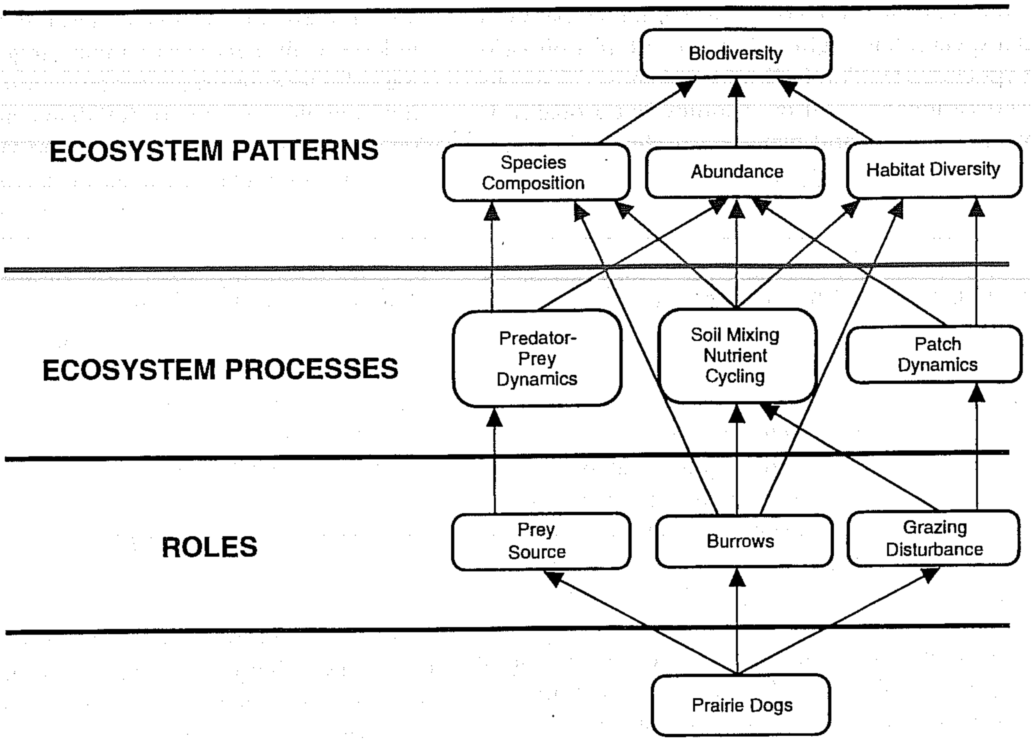

Figure 1. Dominant pathways by which prairie dogs affect ecosystem structure and function.

fossorial mammals, as well as more nomadic ungulates. The disturbance function of prairie dogs becomes even more critical in highly altered prairies that have lost natural disturbance regimes created by fire and large ungulate herds. Consequently, we conclude that prairie dog activities are important to ecosystem integrity and persistence. Thus, even though we found the magnitude of the prairie dog's role was sometimes overstated in the literature, it does meet Paine's qualitative definition of a keystone species.

Power's Keystone Species

Since Paine's original concept was developed, the term keystone has become rather loosely applied and its use in setting conservation priorities has been questioned (Mills and others 1993), leading to an attempt to clarify its definition (Power and others 1996). This new definition has two components: (1) a keystone species has a large overall effect on community or ecosystem structure or function, and (2) this effect is disproportionately large relative to its abundance (Power and others 1996). In addition, Power and others (1996) developed an equation for evaluating per capita effects that provides a quantitative framework for evaluating keystone status. In light of the new keystone definition, we evaluated whether the influence of prairie dogs on ecosystem processes and diversity patterns constitutes large overall effects and whether these effects are large relative to other species in prairie systems.

We begin by assessing whether prairie dogs have a large overall effect on ecosystem structure and function. Although prairie dogs do not consistently increase vertebrate and plant species richness at small scales, they do locally alter species composition and increase landscape-scale diversity by affecting the abundance and distribution of dependent species. In addition, they affect a number of ecosystem-level processes that, in turn, affect landscape heterogeneity and diversity. Individually, none of these functions is particularly large, but collectively they do have a pronounced effect on ecosystem structure and function (Figure 1).

To assess whether these effects can be considered large, we compare the overall impact of prairie dogs to other native herbivores in prairie systems. Prairies are also grazed by ground squirrels and historically were grazed by bison (Benedict and others 1996). Ground squirrels and pocket gophers provide burrows and also serve as prey, although their spatial distribution is typically more dispersed than prairie dogs. The magnitude of the impact of each prairie dog function probably matches or exceeds that of other Great Plains herbivores, but we suggest that none of the other species matches the diverse number of ways prairie dogs influence the system. Furthermore, keystone species

Table 4. Primary consumption of selected herbivores at Badlands National Park

Species	Range area (ha)	Density (per ha)	Mean weight (kg)	Mean daily energy intake (kJ)	Mean daily forage intake (kg-dry wt)	Estimated energy consumption[a] (per kg)	Estimated daily energy consumption (kJ/ha)[b]	Estimated daily dry weight forage consumption (kg/ha)[c]
Black-tailed prairie dog[d]	1300	37.5	1	620	0.053	620	23,250	1.9
Bison[e]	9700	0.04	636	74,250	20.0	117	3,062	0.8
Mule deer[e]	9700	0.023	90	10,766	2	120	244	0.05
Pronghorn[e]	9700	0.021	46	8,618	1.4	187	177	0.03

[a] Mean daily energy intake/mean body weight.

[b] Consumption/kg * density/ha.

[c] Mean daily forage intake * density/ha.

[d] Beckstead 1977; Hansen and Cavender 1973.

[e] Belovsky 1986.

typically function as either predators, prey, mutualists, or habitat modifiers (Mills and others 1993, Power and others 1996). Thus, prairie dogs differ from most conventional keystone species because they fulfill more than one function, acting as prey and modifying the habitat structure and dynamics in several ways. Therefore, we conclude that prairie dogs do indeed have a large overall impact in prairie systems.

To evaluate the second criterion (large effects relative to abundance), we evaluated per capita effects on an ecosystem trait. Operationally, calculation of per capita impacts has a number of difficulties (Power and others 1996). As is the case with most keystone species, experimental data are not available for prairie dogs. Despite this challenge, we conducted a preliminary comparison of per capita disturbance effects using data from Badlands National Park in South Dakota (Beckstead 1977). Black-tailed prairie dogs occupy approximately 12% of the park's 11,000-ha Badlands Wilderness Area, which also supports an intact guild of native ungulate herbivores (bison, mule deer, and pronghorn). Population levels of these species probably reflect historic levels. We estimated per capita primary consumption, standardized by biomass, for each of these four herbivores (Table 4). We also compared primary consumption per hectare. Due to higher basal metabolic rates, primary consumption per kilogram of body weight was greatest for prairie dogs. In addition, the sedentary and colonial behavior of prairie dogs concentrated their activities relative to the more nomadic ungulates; at observed densities, daily consumption per hectare by prairie dogs was at least an order of magnitude higher than any ungulate species. Even if the bison herd size were doubled, prairie dog consumption would still exceed cumulative ungulate consumption. These results indicate that standardized per capita effects of prairie dogs on ecosystem function may meet or exceed the impacts of other herbivores in the Great Plains. We conclude that existing data also meet the criteria of Power and others for keystone species.

Management Implications of Keystone Status for Prairie Dogs

We agree with previous conclusions that prairie dogs are a keystone species that should be targeted for conservation efforts. Prairie dogs have long been controlled on federal, tribal, state, and private lands, primarily at government expense, without any regard for their inherent values (Miller and others 1990). Because keystone status indicates that management for prairie dogs will benefit other species, it provides an important evaluation criterion for balancing two dominant and opposing management themes, prairie dog eradication and conservation. Indeed, keystone status has led public land managers to reevaluate widespread prairie dog eradication programs (Miller and others 1994). It also provides leverage for managers to protect prairie dog habitat when weighing management decisions among multiple uses of public lands and may help to offset the negative view of prairie dogs held by much of the general public.

Even though we agree that prairie dogs have important functions, we caution conservation proponents against overstating the role of prairie dogs. Protective measures for prairie dogs can be justified by existing data that clearly show the disproportionately large effects prairie dogs have on the health and functioning of prairie and shrub-steppe systems. Although dependent, and possibly opportunistic species, can benefit from prairie dog conservation, an inflated list of associated vertebrate species could mislead managers into the

Martin, D. J. 1973. Selected aspects of burrowing owl ecology and behavior. *Condor* 75:446–456.

Mellink, E., and H. Madrigal. 1993. Ecology of Mexican prairie dogs, *Cynomys mexicanus*, in El Manantial, northeastern Mexico. *Journal of Mammalogy* 74:631–635.

Miller, B., C. Wemmer, D. Biggins, and R. Reading. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. *Environmental Management* 14:763–769.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. *Conservation Biology* 8:677–681.

Mills, L., M. E. Soule, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* 432:9–24.

O'Meilia, M. E., F. L. Knopf, and J. C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. *Journal of Range Management* 35:580–585.

Olson, S. L. 1985. Mountain plover food items on and adjacent to a prairie dog town. *Prairie Naturalist* 17:83–90.

Olson, S. L., and D. Edge. 1985. Nest site selection by mountain plovers in northcentral Montana. *Journal of Range Management* 38:278–280.

Olson-Edge, S. L., and W. D. Edge. 1987. Density and distribution of the mountain plover on the Charles M. Russell National Wildlife Refuge. *Prairie Naturalist* 19:233–238.

Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.

Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* 103:91–93.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 466:9–20.

Reading, R. P., S. R. Beissinger, J. J. Grensten, and T. W. Clark. 1989. Attributes of black-tailed prairie dog colonies in northcentral Montana, with management recommendations for the conservation of biodiversity. Pages 13–27 *in* T. W. Clark, D. Hinckley, and T. Rich (eds.), The prairie dog ecosystem: Managing for biological diversity. Montana BLM Wildlife Technical Bulletin No. 2.

Roemer, D. M., and S. C. Forrest. 1996. Prairie dog poisoning in northern Great Plains: An analysis of programs and policies. *Environmental Management* 20:349–359.

Samson, F., and F. L. Knopf. 1994. Prairie conservation in North America. *BioScience* 44:418–421.

Sharps, J. C. 1989. Final report to Rocky Mountain Forest and Range Station. Contract No. 43-82FT-9-0929.

Sharps, J. C., and D. W. Uresk. 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. *Great Basin Naturalist* 50:339–345.

Sheets, R. G., R. L. Linder, and R. B. Dahlgren. 1972. Food habits of two litters of black-footed ferrets. *American Midland Naturalist* 87:249–251.

Steenhoff, K., and M. N. Kochert. 1985. Dietary shifts of sympatric buteos during a prey decline. *Oecologia* 66:6–16.

Tyler, J. D. 1968. Distribution and vertebrate associates of the black-tailed prairie dog in Oklahoma. PhD dissertation. University of Oklahoma, Norman.

Uresk, D. W., and J. C. Sharps. 1986. Denning habitat and diet of the swift fox in western South Dakota. *Great Basin Naturalist* 46:249–253.

Wakely, J. S. 1978. Factors affecting the use of hunting sites by ferruginous hawks. *Condor* 80:316–326.

Weltzin, J. F., S. Archer, and R. K. Heitschmidt. 1997a. Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* 78:751–763.

Weltzin, J. F., S. L. Dowhower, and R. K. Heitschmidt. 1997b. Prairie dog effects on plant community structure in southern mixed-grass prairie. *The Southwestern Naturalist* 42:251–258.

Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778–785.

Woffinden, N. D., and J. R. Murphy. 1977. Population dynamics of the ferruginous hawk during a prey decline. *Great Basin Naturalist* 37:411–425.

Woffinden, N. D., and J. R. Murphy. 1989. Decline of a ferruginous hawk population: A 20-year summary. *Journal of Wildlife Management* 53:1127–1132.

Wuerthner, G. 1997. Viewpoint: The black-tailed prairie dog—headed for extinction? *Journal of Range Management* 50:459–466.

Wydeven, A. P., and R. B. Dahlgren. 1985. Ungulate habitat relationships in Wind Cave National Park. *Journal of Wildlife Management* 49:805–813.

Zarn, M. 1974. Habitat management series for unique or endangered species: Report no. 11, burrowing owl. USDI, BLM, Denver, Technical Note T-N-250.

Zumbaugh, D. M., and J. R. Choate. 1985. Winter food habits of the swift fox on the central High Plains. *Prairie Naturalist* 17:41–47.

Ref

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Biggi

BLACK-FOOTED FERRET-PRAIRIE DOG INTERRELATIONSHIPS

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The black-footed ferret (Mustela nigripes) has been accorded "endangered" status by the U. S. Bureau of Sport Fisheries and Wildlife since 1964. Discovery of ferrets in Mellette County, South Dakota, on a town of black-tailed prairie dogs (Cynomys ludovicianus) led to initiation of a study by personnel of the South Dakota Cooperative Wildlife Research Unit and the South Dakota Department of Game, Fish and Parks (Henderson et al. 1969). Continuing studies led to publications on ferret life history by Hillman (1968) and by Springer (1970); on parasites of the ferret by Boddicker (1968); on burrow systems of prairie dogs by Sheets et al. (1971); and on ferret food habits by Sheets and Linder (1969) and Sheets et al. (1972).

Ferret scats uncovered from burrows of the prairie dog were found by Sheets et al. (1971) to contain chiefly prairie dog remains (91 percent frequency) and remains of mice (26 percent frequency). Hillman (1968) reported that ferrets accepted live-tethered and dead prairie dogs, mice, cottontails, thirteen-lined ground squirrels, and birds placed near the prairie dog burrow they were inhabiting; he also reported that two ferret scats found contained only prairie dog hair and bones, and observed that ferrets had killed prairie dogs, chiefly underground. Henderson et al. (1969) reported that one ferret scat found consisted entirely of prairie dog hair and bones and reported

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[1] Supported jointly by the South Dakota Department of Game, Fish and Parks; U.S. Bureau of Sport Fisheries and Wildlife; South Dakota State University; and The Wildlife Management Institute.

observations of ferrets taking prairie dogs, both dead and alive; they concluded that ferrets lived chiefly in prairie dog towns and depended largely on prairie dogs for their diet.

Since ferrets appear to depend on prairie dogs both for a home and for food, we conducted further studies toward an understanding of ferret-prairie dog relationships. Appreciation is extended to Donald K. Fortenbery, biologist, formerly assigned to ferret studies at Rapid City, for use of his files on sightings of ferrets. The Welder Wildlife Foundation, Badlands Natural History Association, and National Park Service supported early studies by the Unit. The Audubon Society supported work on prairie dog towns in Mellette County in 1972. We are grateful for the cooperation of Maurice E. Anderson, Acting State Supervisor, Division of Wildlife Services, Pierre, South Dakota, for making available records of the former U.S. Bureau of Biological Survey and those of the U.S. Bureau of Sport Fisheries and Wildlife.

METHODS

From June 8 - August 23, 1972, a study was conducted in Mellette County, South Dakota, which consisted of (1) ascertaining the attitudes of landowners toward prairie dogs and ferrets and (2) locating prairie dog towns and mapping and measuring a sample of them. Each rancher in the county was contacted and interviewed concerning locations of prairie dog towns on his land. After the interview, which was conversational, his attitude toward prairie dogs and ferrets that might influence possible ferret management programs was recorded.

Each prairie dog town reported was visited and plotted on a county map. A sample of 40 towns was randomly selected and visited for measurement and more detailed mapping. Depending on the size of the town, the topography on which it occurred, its shape, and its location in relation to natural features, it was mapped using either: 1) several transects paced off to bisect the town; 2) a closed transect by pacing; or, in one instance, 3) a closed-transect by automobile. Prior to survey, counts of prairie dogs above ground were made 2 or 3 times with either 7x50 binoculars or a 20X spotting scope. Weather conditions and time of day were noted at the time counts were made. Counts were averaged, and the average was compared with prairie dog activity curves previously obtained using the percentage of marked prairie dogs above ground under varying conditions and times of the day (Sheets 1970); this comparison yielded an estimate of the total prairie dogs inhabiting the town.

The random sample of 40 towns that were counted and measured was used to estimate the average size of prairie dog towns and the average population of prairie dogs in the county.

Ferret sightings published by Henderson et al. (1969) and Hillman (1971) were combined with those in the files of the Cooperative Wildlife Research Unit, designated as the repository for all ferret sightings in South Dakota since 1966. In addition, Donald Fortenbery, biologist, formerly with the U.S. Bureau of Sport Fisheries and Wildlife at Rapid City, made his file on ferret sightings available to us. Records and correspondence of the Biological Survey and the Division of Wildlife Services, Pierre, were made available and records pertaining to ferrets were extracted from them.

RESULTS

Ferret Distribution

The black-footed ferret is characteristic of the mid- and short-grass prairies. Hall and Kelson (1959) reported that its range nearly coincided with that of prairie dogs (genus Cynomys). It was found from Saskatchewan and Alberta on the north and to the south as far as Texas, New Mexico and Arizona. Henderson et al. (1969) reported that, during the century following discovery of the ferret (Audubon and Bachman 1851), its distribution decreased and that the decline in its numbers resulted from changing land use and control of prairie dogs by poison.

The abundance of the ferret in the past is not known. Because of its nocturnal habits, it is a difficult animal to observe. Except when young are on a prairie dog town, many nights of observation often fail to reveal the presence of a ferret even if one is there. It has been commonly assumed that the ferret was never abundant (Cahalane 1954); however, a biological assistant with the U. S. Bureau of Biological Survey reported that "extensive inquiry brings out the fact that [black-footed] ferrets are not uncommon on the [Indian] reservations of this state [South Dakota] and in certain counties" (monthly report for August dated Sept. 25, 1923).

The following ferrets were mentioned in U.S. Bureau of Biological Survey reports filed at Pierre, South Dakota:

Year	Total Ferrets	Ferrets by Month Month	 Number	 How taken
1917-22	None reported			
1923	1	September	1	trapped (Pine Ridge)
1924	10	September	1	trapped
		October	6	trapped
1925	11	March	2	poisoned
		July	1	trapped
		August	1	trapped
		September	1	trapped
1926	4			
1927	7	March	2	trapped
		April	2	trapped
		August	1	trapped
1928	10	February	1	trapped
		March	5	trapped
		May	1	trapped
1929	1			
1930-39	None reported			

Month and method of capture were not mentioned for all ferrets reported.

With the exception of the ferret taken in September of 1923, the records did not indicate from which area of the state ferrets were taken. A few of the above ferrets were probably placed in the U.S. National Museum and data on them were published by Henderson et al. (1969); however, these authors reported records on only seven ferrets from 1923-29. Since 44 ferrets were reported by men working in ferret-prairie dog range during this 7-year period, ferrets must have been, if not abundant, at least "not uncommon".

Records of ferret sightings in South Dakota were published by Henderson et al. (1969) and by Hillman (1971). These published records, along with those in Table 1, were combined to show the distribution of ferrets in South Dakota (Fig. 1). Ferrets have occurred chiefly in western South Dakota. The greatest number of ferrets were seen in Mellette County, principally because of a concentrated effort to locate

Table 1. Ferret sightings in South Dakota previously unpublished.

County	Year	Animals Seen	Location	Reported or Sighted by	Source
Haakon	1950's	1	S.E. of Midland	Clarence Peterson	N.P.S. report*
Mellette	1952	1	S5, T44N, R30W	J. Burnham	C. Berdan
Bennett	1952-53	1	Near Allen	---	N.P.S. report
Ziebach	1953	1	7 mi. E. of Red Elm	Alfred Halverson	N.P.S. report
Haakon	1954	1	N. of Philip	Jack Wampler	N.P.S. report
Dewey	1960	2	7 W. and 1 N. of Parade	Alfred Halverson	N.P.S. report
Ziebach	1960	1	3 E. and 7 N. of Faith	Alfred Halverson	N.P.S. report
Dewey	1961	1	1 1/2 N. of Isabel	Alfred Halverson	N.P.S. report
Meade	1960-61	1	Plainview	Mrs. Henry McKay	P. Springer
Tripp	1964	1	4 mi. ENE Hammil	Ralph Block	D. Fortenbery
Custer	1965	1	Wind Cave Nat'l Park	W. J. Jellison	D. Fortenbery
Mellette	1965	1	N.W. Mellette Co.	Hans Peterson	D. Fortenbery
Mellette	1965	1	T41N, R31W	Clarence Krogman	D. Fortenbery
Stanley	1965	1	3 S. Oahe Dam	Orville Putzier	D. Fortenbery
Jackson	1966	1	S22, T35N, R21E	Byron Bradfield	D. Fortenbery
Lyman	1966	1	S35, T102, R73	Ralph Block	D. Fortenbery
Mellette	1966	1	S17, T42N, R30W	Conrad Hillman	C. Hillman
Mellette	1967	5 (litter)	S16, T41N, R30W	Conrad Hillman	C. Hillman
Mellette	1967	1	S 10, 11, 14 & 15, T41N, R31W	Raymond Linder	C. Hillman
Pennington	1967	1	1 1/2 W. New Underwood	Jack Hansen	D. Fortenbery
Pennington	1967	1	West end Bombing Range	Ben Thorpe	D. Fortenbery
Perkins	1967	1	S4, T16N, R10W	Alfred Hinds	D. Fortenbery
Shannon	1967	1	S13, W. end Bombing Range	Mike Rock	D. Fortenbery
Mellette	1968	1	E. side White River	Mr. Bartlett	D. Fortenbery
Mellette	1968	5 (litter)	S10, 11, 14 & 15, T41N, R31W	Bob Sheets	C. Hillman
Mellette	1968	1	S10, T42N, R32W	Danny Rasmussen	C. Hillman

Table 1 continued

County	Year	Animals Seen	Location	Reported or Sighted by	Source
Mellette	1968	1	S10, 11, 14 & 15, T41N, R31W	Donald Fortenbery	C. Hillman
Mellette	1968	1	S9, 10 & 11, T41N, R30W	Donald Fortenbery	C. Hillman
Shannon	1968	1	S23, T42N, R42W	George Jonkel	D. Fortenbery
Meade	1969	1	1 E. of Maurine	Pete Haerner	C. Hillman
Mellette	1969	2 (litter)	S10, 11, 14 & 15, T41N, R31W	Bob Sheets	C. Hillman
Mellette	1969	4	S17 & 20, T42N, R27W	Donald Fortenbery	C. Hillman
Mellette	1969	1	3 N. White River	Joe Keever	C. Hillman
Mellette	1970	1	S17 & 20, T42N, R27W	Donald Fortenbery	C. Hillman
Mellette	1970	1	S9, 10, 15 & 16, T40N, R26W	Donald Fortenbery	C. Hillman
Mellette	1970	1	S9, T40N, R32W	Conrad Hillman	C. Hillman
Mellette	1970	2	S7, T41N, R30W	L. A. Krogman	C. Hillman
Custer	1971	1	Wind Cave Nat'l Park	R. Butterfield	C. Hillman
Mellette	1971	3 (litter)	S16, T40N, R32W	Donald Fortenbery	C. Hillman
Mellette	1971	1	S16, T40N, R32W	Donald Fortenbery	C. Hillman
Mellette	1971	3 (litter)	S8, T40N, R32W	Donald Fortenbery	C. Hillman
Mellette	1971	1	S17 & 20, T42N, R27W	Donald Fortenbery	C. Hillman
Mellette	1971	1	S13, T43N, R32W	C. Berdan	C. Berdan
Mellette	1971	1	S8 & 17, T40N, R32W	Littau	C. Berdan
Mellette	1971	1	S13, 14, 23 & 24, T43N, R25W	Vesley	C. Berdan
Butte	1972	1	5 mi. N. E. Newell	Rich Rathert	C. Hillman
Mellette	1972	1	S29, T41N, R26W	Conrad Hillman	C. Hillman
Mellette	1972	1	S16, T40N, R32W	Conrad Hillman	C. Hillman
Mellette	1972	1	S8, T40N, R32W	Conrad Hillman	C. Hillman
Mellette	1972	1	S8 & 17, T40N, R31W	Charles Reed	C. Berdan
Mellette	1972	1	S15, T41N, R26W	M. Koskan	C. Berdan
Mellette	1972	4	S16, T40N, R33W	Conrad Hillman	C. Hillman

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* National Park Service memorandum dated August 3, 1961, reporting on progress of black-footed ferret study during July, 1961, signed by Seasonal Ranger Naturalist John D. Hunter (courtesy Badlands National Monument).

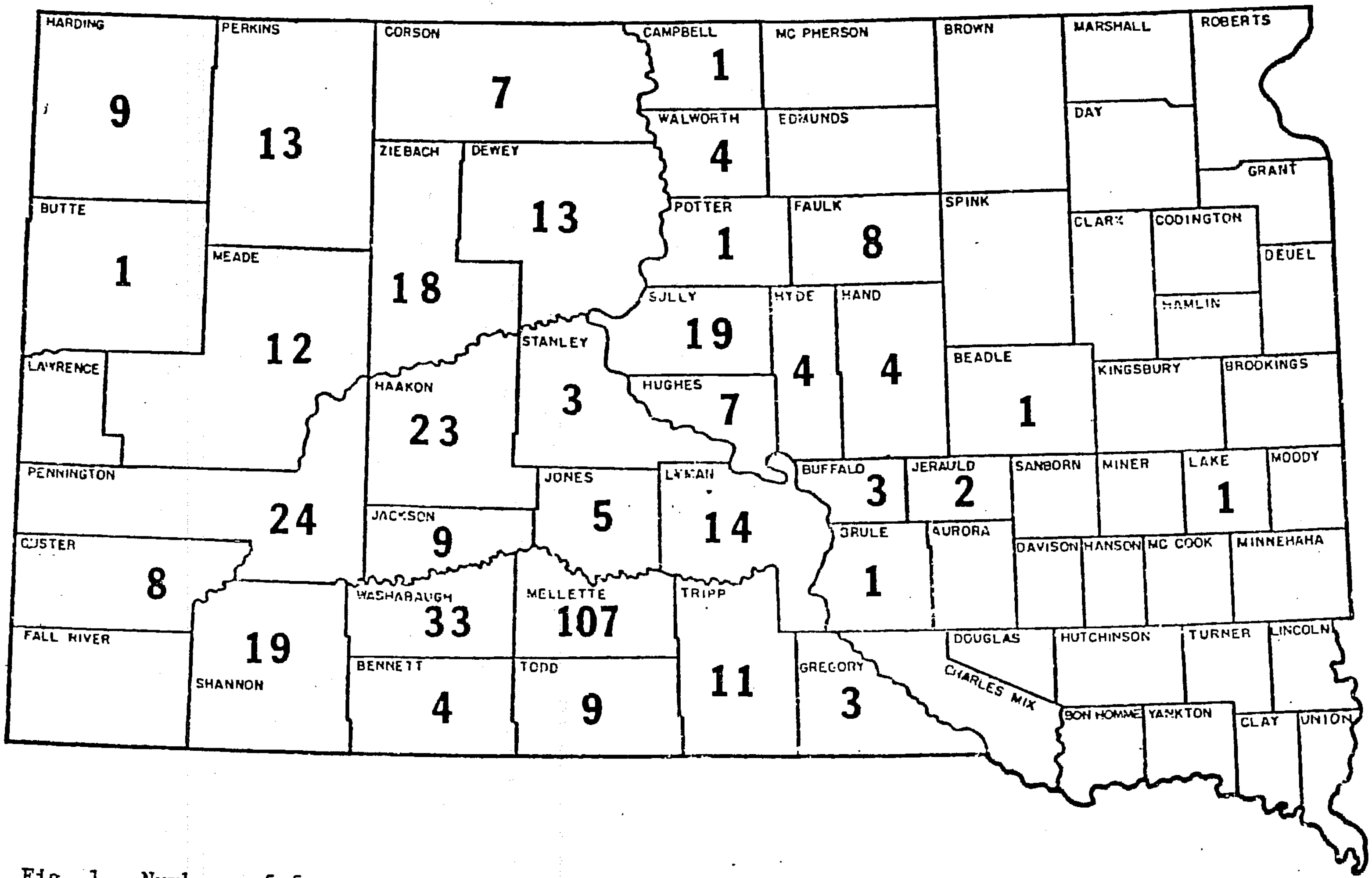

Fig. 1. Numbers of ferrets seen by county in South Dakota, taken both from published and unpublished sources, 1889-1972.

them there since studies by the Unit were begun in 1964. More ferrets were seen in Mellette and Washabaugh Counties than in other counties of the state even prior to 1964. These counties probably represent the area of greatest ferret density in the state.

Prairie Dogs

Several workers have reported an abundance of prairie dogs in North America in the past. Seton (1928) reported that there were probably five billion black-tailed prairie dogs in North America. Merriam (1901) reported there were 400,000,000 prairie dogs on one Texas colony at one time; Seton estimated 800,000,000 in Texas.

Examination of U.S. Biological Survey records for the years 1918 to 1940 gives some indication of prairie dog numbers and control efforts in South Dakota during that period. A Predator Animal Inspector for the U.S. Bureau of Biological Survey, H. R. Wells, estimated that there were 1,756,720 acres of prairie dogs in South Dakota in 1923. Of those acres, 1,283,000 were on private land and 473,720 acres were on public land. This was reduced to an estimated 45,000 acres in the state in 1967 (Henderson et al. 1969).

Control efforts on prairie dogs in South Dakota were intense from 1918 to 1925 (Fig. 2). Intensive control effort was reported for all counties, and in many counties, prairie dogs were considered to have been exterminated.

Control was slackened from 1925 to 1930, partly due to lack of funds, and partly because the emphasis of control was shifted to other rodents such as Norway rats (_Rattus norvegicus_), flickertails (_Citellus richardsonii_) and pocket gophers (_Geomys bursarius_ and _Thymomys talpoides_). These rodents occurred in the cultivated areas of the state and were then considered to be more important than those pests occurring in the rangeland of western South Dakota.

In 1930, effort was again directed toward control of prairie dogs. At that time, many counties reported that prairie dogs were as numerous as before the intensive campaigns began in 1918. Control campaigns using strychnine were initiated during the drought years of the 1930's. Many government programs developed during the depression years were used to control prairie dogs: W.P.A., C.C.C., Indian Emergency Conservation Work, Forest Service in Farm Forestry Programs, Emergency Relief Administration, Resettlement Administration, and Forest Emergency Conservation Work. From 1932 to 1939, over 1,000,000 acres of prairie dog lands were treated. Every county within the prairie dog range in the state reported control efforts. Prairie dogs were reported to have been exterminated in 30 counties (Fig. 3). One report listed all of South Dakota east of the Missouri River as being free of prairie dogs.

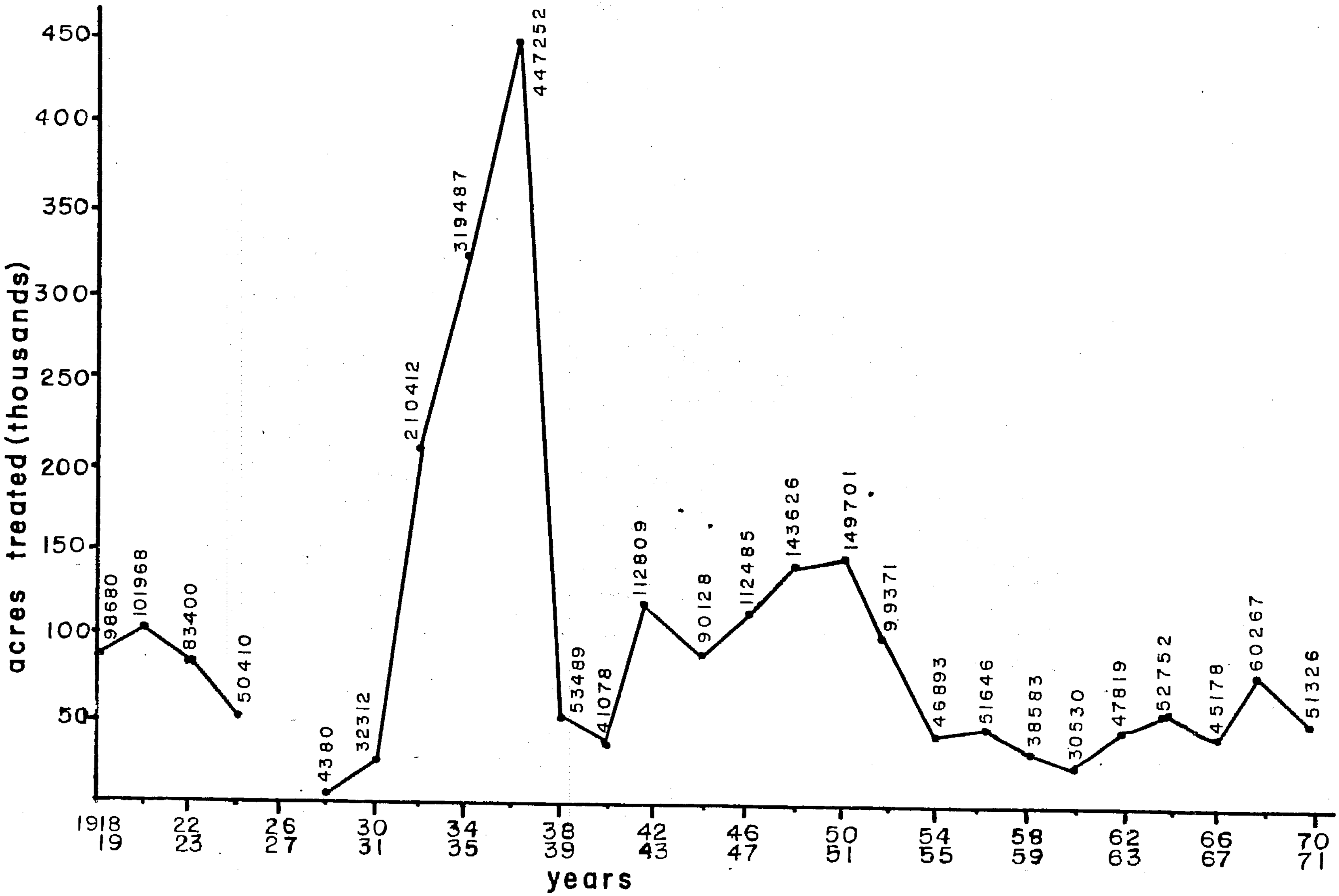

Fig. 2. Acres of prairie dog towns treated with poison bait, South Dakota, 1918-71.

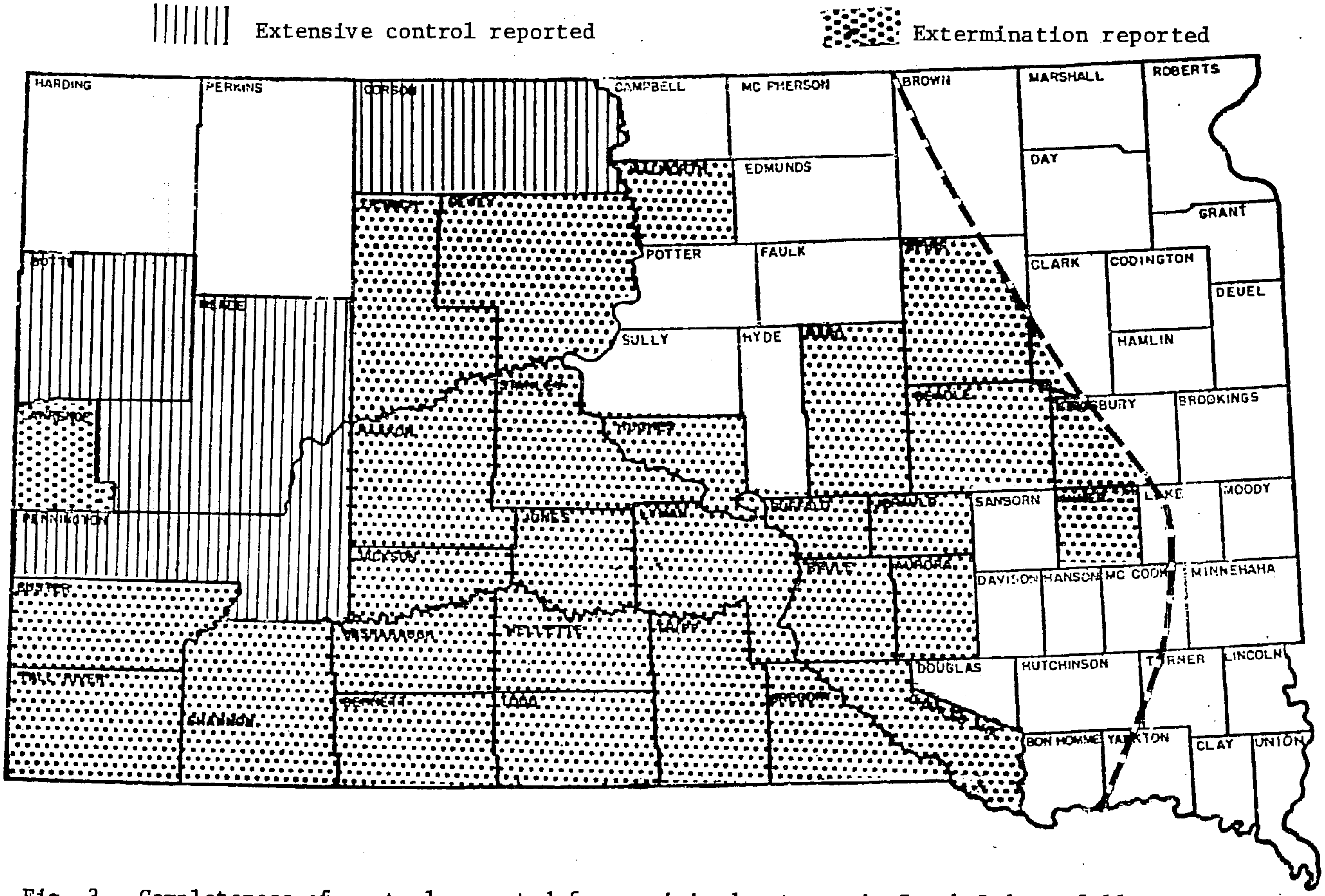

Fig. 3. Completeness of control reported for prairie dog towns in South Dakota following the poisoning campaign of the 1930's. Broken line represents the eastern edge of the prairie dog range.

These extensive poisoning campaigns may have been important in reducing numbers of ferrets as well as prairie dogs. When control was less than complete in a prairie dog town, prairie dogs increased rapidly; this evidently happened after the early 1920's and again following the late 1930's. Control since that time has kept their numbers at a low level. The quantitative effect of extensive poisoning on ferret numbers is not known; however, ferrets have been reported over about the same area in South Dakota in the last 10 years as they occurred in formerly.

Prairie Dogs and Ferrets in Mellette County

Students and biologists assigned to the ferret studies have seen 38 young ferrets in 11 litters and 26 adults since 1964 in Mellette County. These and other observers reported a total of 90 ferrets at different locations in the past 10 years in the county. Of course, only a small proportion of the ferrets probably were seen and/or recorded. Much of the time spent in attempting to make ferret observations was on the Carr (now Nielsen) Ranch about 12 miles west of White River. Other efforts were centered in the southwest and western portion of the county; relatively little time was spent east of White River. However, ferret sightings were made in all parts of the county.

Numbers of prairie dogs have varied considerably in the county. In 1929, an employee of the U.S. Biological Survey estimated that there were 47,000 acres of prairie dog towns in Mellette County. Henderson et al. (1969) estimated 2,000 acres of prairie dog towns in the county for 1967. During the past summer, we attempted to locate all prairie dog towns in the county. We found 151 towns (Fig. 4); their average size was 21 acres. We estimated that there were 239 prairie dogs per town, for a population of 36,000 in the county.

The prairie dog towns in Mellette County (Fig. 4), totaling about 3171 acres, appear to be maintaining a ferret population. Ferrets have been observed in most parts of the county. In the southwest region of the county, there is considerable cropland with small prairie dog towns interspersed in the pastures. For several consecutive years, ferrets have been observed there. In the area south and west of White River on the Carr (now Nielsen) Ranch, ferrets were studied from 1966 to 1969. There was a litter each of 3 years on a 107-acre town and one other litter on a 64-acre town on the ranch. This region is all grassland and badlands type with few prairie dog towns, but the towns are large. We have also seen ferrets in the eastern part of the county, where more land is used for crops. Some observations of ferrets were made on small towns (under 10 acres) and some on larger towns.

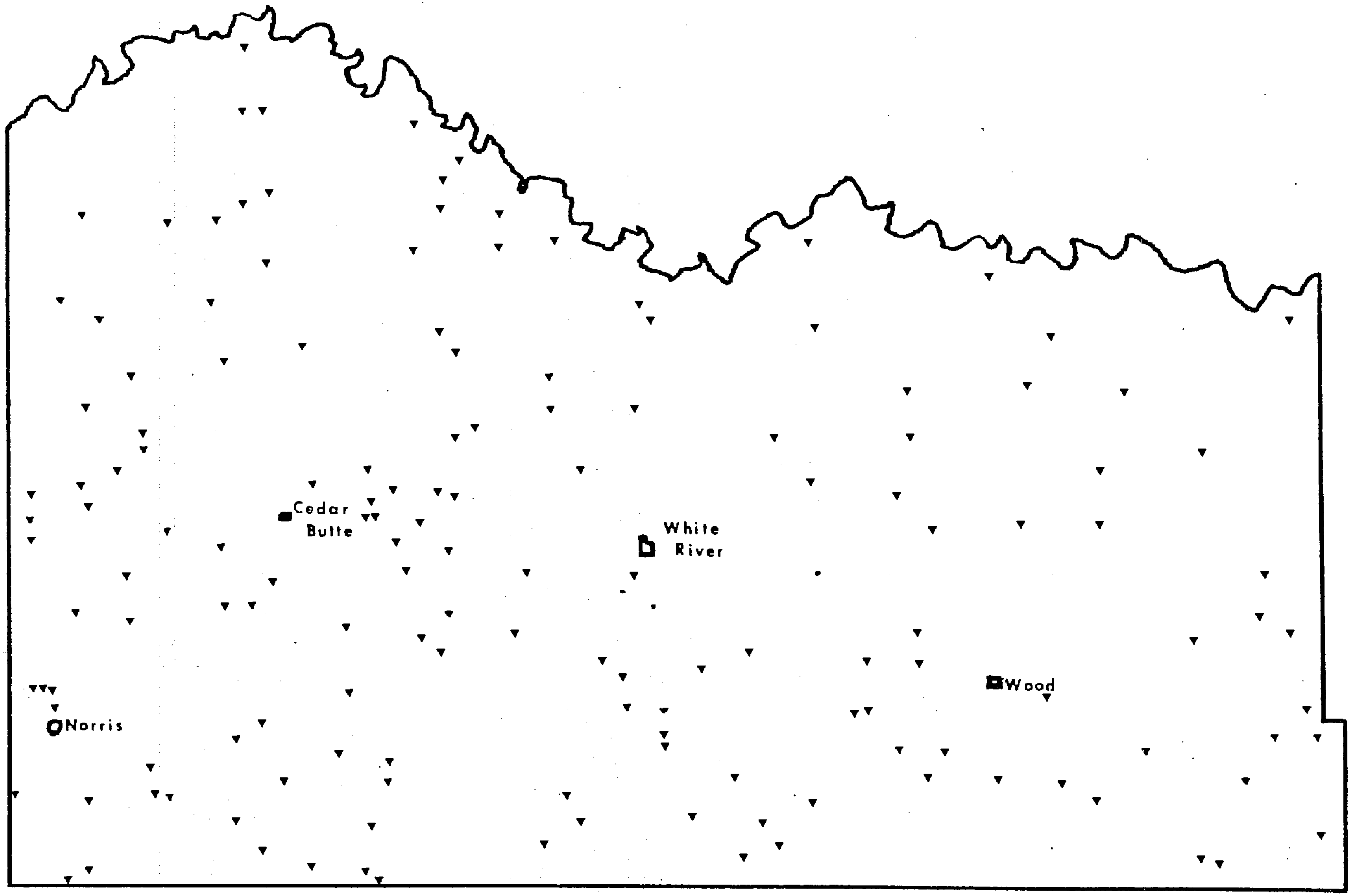

Fig. 4. Distribution of 151 active prairie dog towns in Mellette County, South Dakota, 1972.

MANAGEMENT

Because the ferret is chiefly dependent upon the prairie dog for shelter and diet, management in favor of prairie dog populations in ferret-occupied areas is management in favor of ferret populations.

Proposals for management of ferrets have been suggested by previous workers. Henderson et al. (1969) listed 10 recommendations. Included in those recommendations were (1) "explore all feasible means of retaining adequate numbers of prairie dogs and ferrets on both public and private lands," (2) "experiment with transplanting and releasing ferrets into areas where prairie dogs are protected," and (3) "develop materials for prairie dog and other animal control that will not poison ferrets." The Trail (published by the National Audubon Society and the North Central Audubon Council, 1972) editorialized that a "prairie dog bank" might be in order, following the same pattern as the "water bank" or the "soil bank."

In interviews with Mellette County ranchers, 19 percent were against having any prairie dogs, 19 percent were against any poisoning of prairie dogs, and 62 percent of them stated they would like to have prairie dog towns if they could keep the towns from becoming too large. Thus, techniques to control prairie dog numbers that would be safe for ferrets are needed. Such a technique might be the use of reproductive inhibitors. Preliminary work by a graduate student of the Unit indicates that this may be a useful technique (Pfeiffer 1972), but further work needs to be done.

A transplanting program or a captive-breeding program for restocking ferrets might be feasible. One of the most valid objections to any restocking program is that restocking is usually not effective because the habitat for the species is absent or curtailed. However, for the ferret, much habitat is available in the form of prairie dog towns in the western half of South Dakota. There are areas in South Dakota where prairie dogs occur but where ferrets have not been reported, even after extensive searches.

We have managed game species for years by developing or preserving habitat; some of these game management techniques should be useful for ferrets. Gates (1970) proposed that wetlands interspersed in the farmlands be preserved for pheasant habitat. Hamerstrom et al. (1957) recommended a "scatter-pattern" of 40 acres per section managed for prairie chickens in Wisconsin where that species was endangered. A scattered distribution of prairie dog towns may be important to the ferret.

In Mellette County there are approximately 3200 acres of prairie dog towns. It appears that this many acres of prairie dog towns has been adequate as habitat and food supply for ferrets. These prairie dog towns could be administered similar to wetlands in present waterfowl programs; instead of "Waterfowl Production Areas" they could be "Ferret Production Areas."

Prairie dog towns could be preserved by purchase, lease or easements. An estimate of the value of grazing land in Mellette County is about $50.00 per acre (Westin et al. 1971). Thus, the purchase price of land occupied by prairie dogs would be $160,000. Current lease value of grasslands in the county is about $3.00 per acre, so leasing the prairie dog towns would cost $9,600 annually. Easements would be even less in cost.

Easements of prairie dog towns would perhaps be the most practical method. With an easement to preserve prairie dog towns on his land, the rancher could continue grazing the towns in a normal manner. Grazing by cattle is probably beneficial in maintaining the towns. It would be necessary to stipulate in the terms of the easement that prairie dogs could not be eliminated or controlled by using any methods that might be detrimental to ferrets. Shooting on towns could be permitted and would furnish sport to the rancher and his friends. With an easement arrangement, the rancher could be compensated for an increase in size of dog towns if he chose not to control their expansion.

By obtaining an easement on prairie dog towns in an area where ferrets exist, we would have some assurance that ferrets could be maintained until further research could be used to answer some of the questions involved in ferret management. One of the prime objectives of research should be to determine the sizes, numbers, and spatial distribution of prairie dog towns necessary to maintain ferret populations. Such research would be important for possible expansion of the range of the black-footed ferret into areas now occupied by the prairie dog in North America.

LITERATURE CITED

Audubon, J. J., and J. Bachman. 1851. The viviparous quadrupeds of North America. Vol. II. V. G. Audubon, New York. 334pp.

Boddicker, M. L. 1968. Parasites of the black-footed ferret. Proc. S. Dak. Acad. Sci. 47:141-148.

Cahalane, V. H. 1954. Status of the black-footed ferret. J. Mammal. 35(3):418-424.

Gates, J. M. 1970. Recommendations for a scattered wetlands program of pheasant habitat preservation in southeast Wisconsin. Research Report 63. Wisconsin Department of Natural Resources. 24pp.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. The Ronald Press Co., New York. 1082pp.

Hamerstrom, F. N., Jr., O. E. Mattson, and F. Hamerstrom. 1957. A guide to prairie chicken management. Tech. Wildl. Bulletin Number 15. Wisconsin Conservation Department. 128pp.

Henderson, F. R., P. F. Springer, and R. Adrian. 1969. The black-footed ferret in South Dakota. S. Dak. Dept. Game, Fish and Parks Bull. 37pp.

Hillman, C. N. 1968. Field observations of black-footed ferrets in South Dakota. Trans. N. Am. Wildl. and Nat. Resources Conf. 33:433-443.

____________. 1971. The black-footed ferret. S. Dak. Conservation Digest. 38(4):5-7.

Merriam, C. Hart. 1901. The prairie dog of the Great Plains. U.S. Dept. Agr. Yearbook. p. 257-270.

Pfeiffer, D. G. 1972. Effects of diethylstilbestrol on reproduction in the black-tailed prairie dog. M.S. thesis, South Dakota State University, Brookings. 42pp.

Seton, E. T. 1928. Lives of game animals. Vol. IV. Doubleday, Doran and Co., Inc. Garden City, New York. 949pp.

Sheets, R. G. 1970. Ecology of the black-footed ferret and the black-tailed prairie dog. M.S. thesis, South Dakota State University, Brookings. 42pp.

____________, and R. L. Linder. 1969. Food habits of the black-footed ferret (Mustela nigripes) in South Dakota. Proc. S. Dak. Acad. Sci. 48:58-61.

____________, ____________, and R. B. Dahlgren. 1971. Burrow systems of prairie dogs in South Dakota. J. Mammal. 52(2):451-453.

____________, ____________, and ____________. 1972. Food habits of two litters of black-footed ferrets in South Dakota. Am. Midl. Natural. 87(1):249-251.

Springer, P. F. 1970. The black-footed ferret. In Alive in the wild, edited by Victor H. Cahalane. Prentice-Hall, Inc. p. 86-91.

The Trail. 1972. Endangered species in the north midwest. The National Audubon Society and the North Central Audubon Council. Vol. 8(1):1.

Westin, F. C., M. Stout, D. L. Bannister, F. T. Miller, and C. J. Frazee. 1971. Relationships between land sales figures, soils, and crop yields as a guide for agricultural land evaluation. Cooperative Extension Publ. ESS-12, South Dakota State University, Brookings. 6pp.

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In answer to questions, Dr. Linder added that the availability of ferrets for transplants is still uncertain. He said that Patuxent has been working with domestic ferrets in preparation for attempts to raise black-footed ferrets in captivity.

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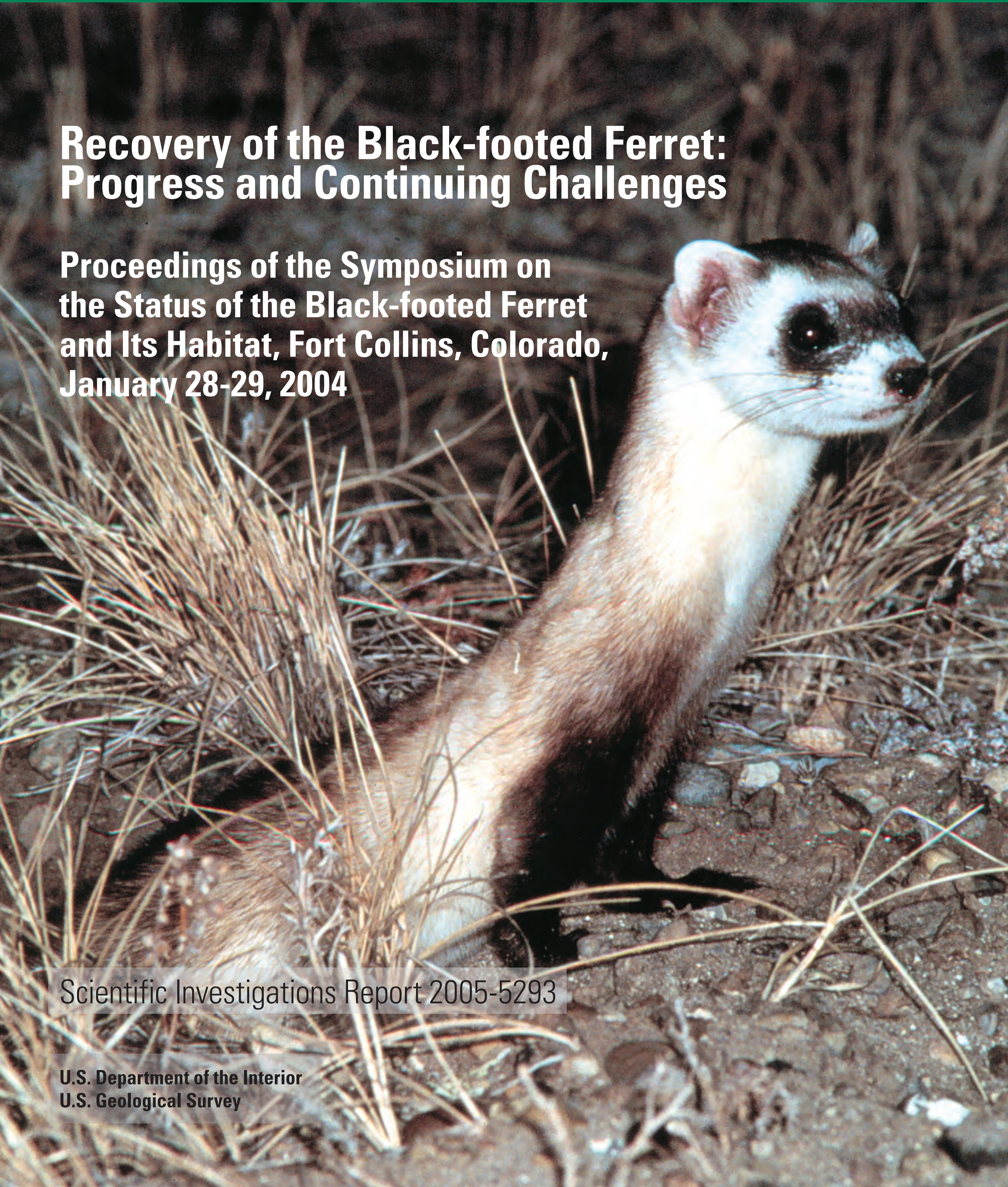

Recovery of the Black-footed Ferret: Progress and Continuing Challenges

Proceedings of the Symposium on the Status of the Black-footed Ferret and Its Habitat, Fort Collins, Colorado, January 28-29, 2004

Scientific Investigations Report 2005-5293

U.S. Department of the Interior
U.S. Geological Survey

Cover photo of black-footed ferret by Dean Biggins taken on
East Core Prairie Dog Colony, Meeteetse, Wyo., February 1983


Heather Bramick
1999

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Edited by James E. Roelle, Brian J. Miller, Jerry L. Godbey, and Dean E. Biggins

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U.S. Department of the Interior
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Contents

Acknowledgments

The Symposium on the Status of the Black-footed Ferret and Its Habitat, held January 28–29, 2004, in Fort Collins, Colo., and the resulting proceedings contained herein would not have been possible without the dedicated efforts of numerous individuals and agencies. Financial support for the meeting itself and for publication of this volume was provided by Aaron and Gretchen Clark of the Black-footed Ferret Recovery Foundation, by the U.S. Fish and Wildlife Service, and by the U.S. Geological Survey. Sandi Godbey, ably assisted by Jenny Benson, Matt Dunfee, Darren Long, Noe Marymor, Adam Phillips, Adrianna Siniawski, and Ashley Skeen, attended to the infinite variety of details that make a meeting run smoothly. We gratefully acknowledge Dr. Andrew Dobson, Princeton University, Department of Ecology and Evolutionary Biology, for the keynote address, as well as the assistance of Della Garelle, Mike Lockhart, Bill Van Pelt, and Chris Brand, who served as session moderators. We thank Mike Lockhart, Paul Marinari, and Julie Kreeger for hosting a field trip to the National Black-footed Ferret Conservation Center, which at the time of the symposium was under construction but is now a fully functioning facility. We are indebted to Dale Crawford, Delia Story, Jennifer Shoemaker, and especially Dora Medellin for their able assistance in preparing the text and graphics for publication and to Heather Branvold, Patricia Mendoza, and Dale Crawford for graciously allowing us to use their artwork. Finally, we wish to thank the many organizations and countless individuals who have contributed to the Black-footed Ferret Recovery Program. While space does not allow us to mention them individually, it is obvious that neither the symposium nor this volume would have been possible without their unflagging efforts on behalf of one of North America's most engaging creatures.

Dedication

In the period between January 2004, when this symposium took place, and publication of the proceedings presented here, partners in the Black-footed Ferret Recovery Program suffered enormous personal and professional losses through the deaths of Tom Thorne, Beth Williams, Bill Russell, and Stan Anderson.

Tom and Beth, a husband and wife team of professional veterinarians and wildlife biologists, were killed in a traffic accident on their way home to Laramie, Wyo., on December 29, 2004. Both Tom and Beth were responsible for much of the original recovery program leadership and were deeply involved in all elements of black-footed ferret management and research. Their expertise and many notable scientific contributions significantly advanced our knowledge and capabilities related to black-footed ferret captive breeding, disease risks and management, vaccine efficacy and safety, and reintroduction.

Bill Russell died at Ivinson Hospital in Laramie on August 16, 2005. Bill was a Professor of Animal Science at the University of Wyoming for 25 years and was the official Black-footed Ferret Species Survival Plan® studbook keeper and genetic advisor for many years. Bill provided invaluable advice and recommendations on captive black-footed ferret management and breeding.

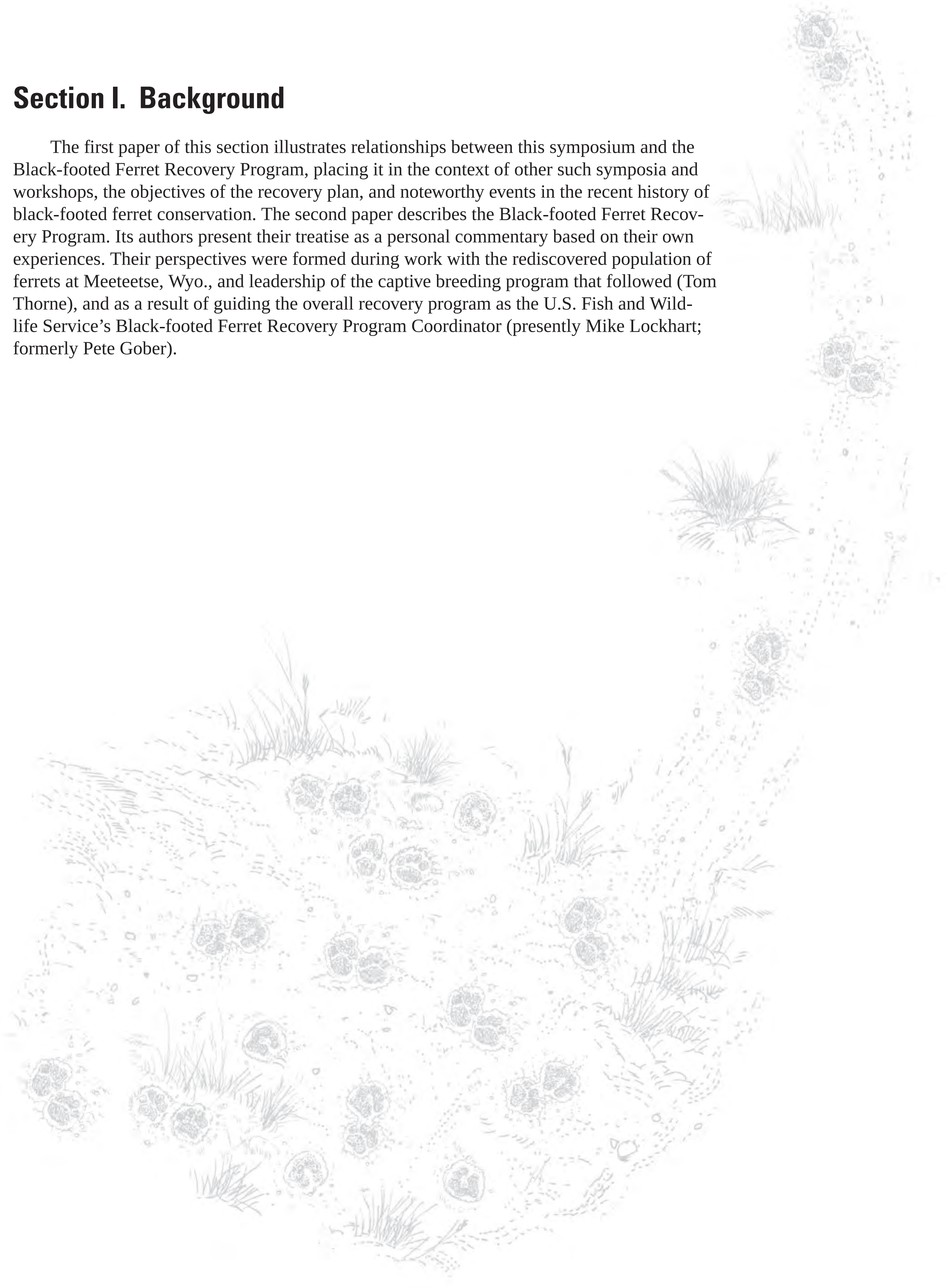
Stan Anderson died at his home in Laramie on September 1, 2005, following an extended illness. Stan started the University of Wyoming Cooperative Fish and Wildlife Research Unit in 1980 and served as a graduate advisor for many biologists who obtained advanced degrees studying various aspects of prairie dog conservation and black-footed ferret recovery.

These proceedings are dedicated to the memory and accomplishments of these long-time ferret recovery advocates, scientists, advisors, administrators, and mentors. The loss of these fine individuals leaves a substantial void in the institutional knowledge and foundation of the Black-footed Ferret Recovery Program and in the wildlife conservation community as a whole. They will be deeply missed, but their legacy will endure.


Heather Bramald
'08

Section I. Background

The first paper of this section illustrates relationships between this symposium and the Black-footed Ferret Recovery Program, placing it in the context of other such symposia and workshops, the objectives of the recovery plan, and noteworthy events in the recent history of black-footed ferret conservation. The second paper describes the Black-footed Ferret Recovery Program. Its authors present their treatise as a personal commentary based on their own experiences. Their perspectives were formed during work with the rediscovered population of ferrets at Meeteetse, Wyo., and leadership of the captive breeding program that followed (Tom Thorne), and as a result of guiding the overall recovery program as the U.S. Fish and Wildlife Service's Black-footed Ferret Recovery Program Coordinator (presently Mike Lockhart; formerly Pete Gober).



The Symposium in Context

By Dean E. Biggins[1]

The black-footed ferret (*Mustela nigripes*) is a member of the weasel family (Mustelidae) and is closely related to the Siberian polecat (*M. eversmannii*) of Asian steppes and the European polecat (*M. putorius*). Compared to its relatives, the black-footed ferret is an extreme specialist, depending on the prairie dogs (*Cynomys* spp.) of North American grasslands for food and using prairie dog burrows for shelter. The black-footed ferret's close association with prairie dogs was an important factor in its decline. Prairie dogs were regarded as an agricultural pest as human settlement progressed westward, and they became important hosts for plague as that disease colonized eastward from its sources of introduction on the west coast. Prairie dog numbers were dramatically reduced by poisoning, cropland conversions, and plague during the first half of the 20th century, and black-footed ferret populations declined precipitously. The black-footed ferret was included on the first lists of endangered species, and its status was precarious by the time the Endangered Species Act of 1973 was passed. Its rebound from a low point of 10 known individuals in spring of 1985 (Biggins and others, 2006) is impressive, but the species is not yet "recovered" in either the biological or legal sense (for further details, see Lockhart and others, this volume).

Conservation activities to assist black-footed ferrets have extended through the past five decades. Included in those activities were three previous workshops and a symposium organized to facilitate interchange of ideas and information. The contents of their published proceedings illustrate changes in emphasis regarding issues important to black-footed ferret recovery. Placing these meetings in a chronological context of major events in ferret conservation (fig. 1) helps to explain motives for convening them and content of the papers, and provides context for the current volume.

The first workshop on black-footed ferrets and prairie dogs (Linder and Hillman, 1973) focused primarily on the rangewide status of the ferret and its prairie dog habitat, with

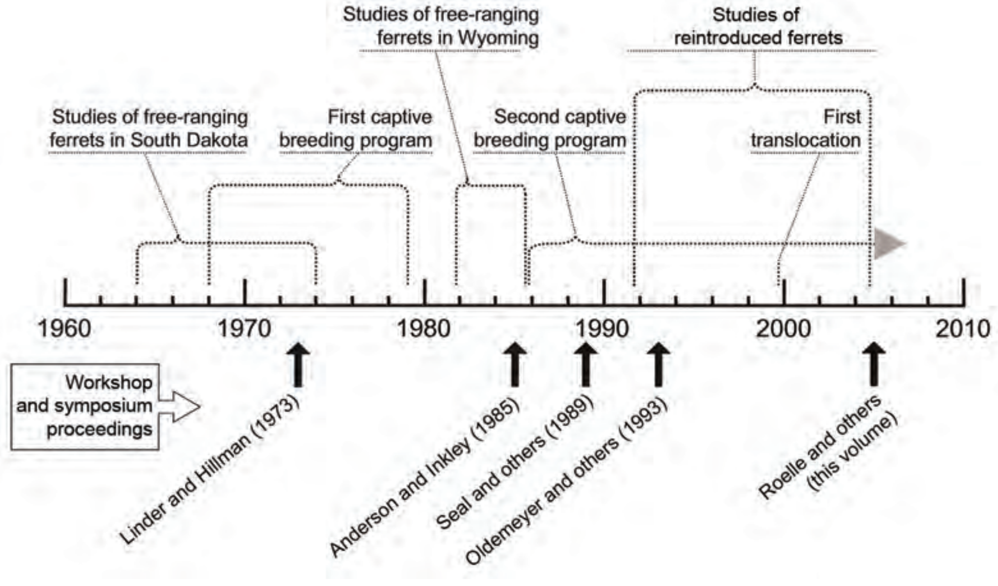


Figure 1. Timeline relating recent symposia and workshops to noteworthy events and periods in black-footed ferret (*Mustela nigripes*) research and recovery.

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[1] U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Ave., Bldg. C, Fort Collins, CO 80526.

a single paper summarizing new information on the biology of the ferret. Despite 10 years of research on the black-footed ferret in South Dakota (fig. 1), Ray Erickson concluded that it remained "one of the least well known of all of the endangered mammals of the United States" (Erickson, 1973, p. 156). Rumors began circulating in the late 1970s that the black-footed ferret was extinct, but these contentions were short-lived because of the discovery of a population of ferrets near Meeteetse, Wyo., in 1981 (Biggins and others, 2006).

The second workshop on black-footed ferrets (Anderson and Inkley, 1985) occurred near the end of a rather brief period of intensive research on the Meeteetse population of ferrets and after the first attempt to captive breed South Dakota ferrets at the U.S. Fish and Wildlife Service's (now U.S. Geological Survey's) Patuxent Wildlife Research Center in Maryland (fig. 1). A single paper in that workshop was devoted to captive breeding, summarizing the failed Patuxent attempt but prophetically predicting success if the venture were to be repeated with ferrets from the Meeteetse population (Carpenter, 1985). The proceedings had a wide variety of other papers on the status of prairie dogs and ferrets, institutional and procedural issues, searches for more ferrets, and research needs. Six papers summarized original field research, much of which was conducted on the Meeteetse population. By summer of 1985, 10 months after the workshop, plague caused extensive declines in the Meeteetse prairie dog population, canine distemper was discovered in the ferrets, and the ferret population plummeted. These events caused an abrupt end to field research on ferrets and forced the beginning of the second captive breeding program following emergency rescue of the remaining animals. Carpenter's (1985, p. 12.11) admonition (presumably motivated in part by his Patuxent experience) to avoid the "tendency to initiate propagation programs as a last resort, when few animals are available for captive breeding" could not be heeded. Research at Meeteetse also served as the primary motivation for publication of a second collection of black-footed ferret papers the following year as number 8 of the Great Basin Naturalist Memoirs (Wood, 1986), although that volume was not the result of a symposium or workshop.

The third workshop, held in 1986, was conceived primarily in response to information needs for the newly developing second effort to maintain and produce black-footed ferrets in captivity (fig. 1). It blended developing theories in conservation biology with existing biological information on ferrets and polecats. This workshop resulted in a book (Seal and others, 1989) with chapters covering systematics, population biology, reproduction, captive propagation, and conservation.

The fourth meeting was a symposium convened in the summer of 1989. Although the captive breeding program had a tenuous beginning (Biggins and others, 2006; Lockhart and others, this volume), evidence predicting ultimate success had emerged by 1988, and thoughts were turning toward planning for reintroduction. Reports in the proceedings (Oldemeyer and others, 1993) focused primarily on habitat for reintroduction of ferrets. Plague received increased recognition as an ominous threat to ferret habitat, with several papers dedicated to discussion of that disease.

The symposium culminating in the papers presented herein was held on January 28–29, 2004, in Fort Collins, Colo. It had been more than 10 years since the previous symposium, and much new information on the biology of the black-footed ferret had been accumulated. Many of the papers published here resulted from information collected as captive breeding became more efficient and as black-footed ferrets were released back into native habitats (fig. 1). The symposium was organized into sections based on the principal topics in the stepdown outline of the Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988). The relationship between the recovery plan and the papers of this symposium illustrates that work is following a somewhat orderly progression guided by principal topics in the recovery plan. A brief description of that relationship introduces each section of this volume.

This volume and the five that preceded it, including proceedings from the three workshops and the symposium, plus the Great Basin Naturalist volume (Wood, 1986), cover a broad spectrum of work on prairie dogs and black-footed ferrets. Although these volumes certainly are not exhaustive in their coverage of ferret and prairie dog research and conservation activities, they collectively provide a solid foundation for future conservationists working with ferrets and chronicle a long-term recovery program for one of North America's most endangered vertebrates.

References Cited

Anderson, S.H., and Inkley, D.B., eds., 1985, Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 1.1–33.12.

Biggins, D.E., Miller, B.J., Clark, T.W., and Reading, R.P., 2006, Restoration of an endangered species—the black-footed ferret, *in* Groom, M.A., Meffe, G.K., and Carroll, C.R., eds., Principles of conservation biology (3d ed.): Sunderland, Mass., Sinauer Associates, p. 581–585.

Carpenter, J.W., 1985, Captive breeding and management of black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 12.1–12.13.

Erickson, R.C., 1973, Some black-footed ferret research needs, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 153–164.

Linder, R.L., and Hillman, C.N., preparers, 1973, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, 208 p.

Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., 1993, Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, 96 p.

Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., 1989, Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, 302 p.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

Wood, S.L., ed., 1986, Great Basin Naturalist Memoirs No. 8: Provo, Utah, Brigham Young University, 208 p.

A Historical Perspective on Recovery of the Black-footed Ferret and the Biological and Political Challenges Affecting Its Future

By J. Michael Lockhart,[1] E. Tom Thorne,[2] and Donald R. (Pete) Gober[3]

Abstract

This paper is a personal commentary by the authors on the background and historical development of the Black-footed Ferret Recovery Program. The black-footed ferret (*Mustela nigripes*) was recognized as imminently endangered in the original Endangered Species Act and has a recovery history accentuated with near catastrophes and remarkable successes. In this paper, we examine the species' near demise, wild black-footed ferret populations, captive breeding efforts, and attempts to restore ferret populations into native habitats. We provide our personal perspectives on many lessons learned during these program stages, the social and political factors affecting species recovery, past and present biological obstacles, and insights relevant to the future of the species.

Keywords: black-footed ferret, captive breeding, endangered species, *Mustela nigripes*, recovery, reintroduction

Introduction

Rather than a technical presentation of data or a literature review, this paper is a personal commentary on historical aspects of the Black-footed Ferret Recovery Program. We offer our recollections and observations only as reflections of our own experiences. We acknowledge that many people contributed to black-footed ferret (*Mustela nigripes*) conservation over this period and that others may view program events and our conclusions differently; however, we submit that our unique positions of program responsibility over the years provide broad perspectives that others not directly involved in day-to-day ferret recovery, or involved in limited areas, may not have gained.

Collectively, as representatives of lead agencies responsible for ferret recovery, we have been directly involved in ferret conservation matters on a daily basis from 1981 to the present. The Wyoming Game and Fish Department (WGFD) was a primary participant in ferret recovery both in the field and in captive breeding from 1981 to 1996 and remains active in reintroduction and program planning activities today. The U.S. Fish and Wildlife Service (FWS) has been involved with ferret conservation since before the species was originally listed as endangered in 1967. Moreover, FWS has been directly involved with captive breeding since 1996 and has coordinated all other recovery activities since that time. In addition, FWS has investigated the likely effects of habitat loss on ferrets as a result of the decline of its principal prey—prairie dogs (*Cynomys* spp.).

In this paper, we discuss ferret conservation activities related to wild population management, captive breeding, and reintroduction into the wild. In particular, we address the significant biological, political, and social issues that affected species recovery. We focus only on the major highs and lows of ferret recovery as we view them; we defer the many important details to other participants in this symposium. Additionally, we characterize our observations of various efforts as successes, failures, or lessons learned. Finally, we provide recommendations linked to these conclusions that may contribute to future recovery of ferrets and perhaps other endangered species.

The opinions and recommendations presented in this paper are those of the authors and do not represent official positions of either the FWS or the WGFD. We also wish to acknowledge the extraordinary dedication, hard work, and contributions accomplished by the many State, Federal, tribal, zoo, and conservation organization partners on behalf of black-footed ferret recovery. Overall program success is the result of enormous efforts by these many program cooperators.

Management of Free-ranging Populations

Ferrets received little attention until the species was listed as endangered in 1967, one of several species to be designated under the first version of the Endangered Species Act (ESA). Early accounts, from Audubon's description of the type

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specimen in the 19th century to anecdotes from rodent control personnel in the mid-20th century, largely treated the species as a novelty. Its secretive and nocturnal lifestyle in remote parts of western North America assured relative anonymity. Conversely, the ferret's principal prey received much more attention: prairie dogs were regarded as vermin, competitors with the agriculture industry, and impediments to western settlement. Accordingly, prairie dog populations were targeted for destruction, and decades of eradication efforts significantly impacted populations of prairie dogs and ferrets, the prairie dog's most highly specialized obligate predator.

Five species of prairie dogs occur in North America. Three of these species cover most of the collective prairie dog (and ferret) historical range: the black-tailed prairie dog (*C. ludovicianus*), the white-tailed prairie dog (*C. leucurus*), and the Gunnison's prairie dog (*C. gunnisoni*). No documented occurrence of ferrets has been linked to either the Utah prairie dog (*C. parvidens*) or the Mexican prairie dog (*C. mexicanus*). These two species have ranges that are relatively small and disjunct from those of the other three prairie dog species. Black-tailed prairie dogs occurred over the largest expanse of land (approximately 160 million ha), from southern Canada to northern Mexico between the 98th meridian and the Rocky Mountains. White-tailed prairie dogs and Gunnison's prairie dogs occurred over approximately 80 million ha to the west of the range of the black-tailed prairie dog. Perhaps 10–20 percent of the range of all of these prairie dog species was physically occupied before western settlement. The actual location of prairie dogs varied with topography, soils, rainfall, fire, bison (*Bison bison*) activity, and other factors. Regardless of the dynamics of these important and variable biological and ecological phenomena, it is obvious that ferrets had an enormous habitat base, and many thousands undoubtedly existed across the landscape.

Ferret populations declined over millions of hectares of occupied prairie dog habitat for three principal reasons. First, a major conversion of native prairie to cropland began late in the 19th century, continued steadily through the Dust Bowl years of the 1930s, and to a lesser extent continues today. Approximately one-third of black-tailed prairie dog potential habitat was rendered useless for prairie dogs by cropland conversion. In comparison, far less of the available habitat of white-tailed and Gunnison's prairie dogs was physically lost to land conversion because, outside of riparian corridors and proximate irrigated lands, much of the habitat occupied by these species is not suitable for crops.

Second, poisoning of prairie dogs as a means of reducing competition with domestic livestock for forage accelerated with agricultural policies in the United States around the time of World War I. Significant Federal funds became available for poisoning programs across the West from approximately 1918 to 1971, after which the use of many of these chemical rodenticides was banned. Tens of millions of hectares of occupied prairie dog habitat were eliminated during this period. Many poisoned prairie dog complexes have never recovered to levels that could support ferret populations.

Third, the exotic disease sylvatic plague, foreign to the evolutionary history of prairie dogs, was inadvertently introduced into North America around 1900. The impact of this disease on prairie dogs and ferrets has been significant. Plague has been documented over all of the ranges of the three principal prairie dog species, except for approximately the eastern third of the black-tailed prairie dog range.

Biologically, the prairie dog ecosystem was devastated by factors described above, and the consequences to ferret populations were even greater. Politically, failure to consider the ramifications of these impacts also resulted in diminished populations of many other species and in several cases led to later consideration of further regulatory protection, such as listings under the ESA. Socially, the domination of farming and ranching activities on most lands in the American West has more severely impacted some species than others. The nadir of occupied prairie dog habitat probably occurred around 1971, when certain toxicants were banned for prairie dog poisoning. Many poisoned prairie dog populations apparently have increased severalfold since that time but remain low relative to historical numbers. Nevertheless, the limited recovery of some prairie dog populations is important in the context of potential ferret recovery and long-range management.

Ferret occurrence undoubtedly mirrored fluctuations in prairie dog populations. Steadily declining numbers of credible ferret sightings occurred during the 1950s and 1960s. The last population of a few dozen animals was thought to have been located in Mellette County, S. Dak., in 1964 (fig. 1). This population was studied through 1974, and a few animals were captured for a captive breeding trial (see below).

Biologically, the initial field studies of wild ferrets in South Dakota provided a starting point for later reintroduction efforts—a small success; however, this population continued to decline in the face of reduced and progressively fragmented habitat. The political will to conserve this individual population through regulatory action did not exist in the era preceding passage of the ESA. This lack of action represented a notable conservation failure inasmuch as, however difficult the challenges of recovering wild populations in native habitat may be, those challenges pale in comparison to the trauma, demands, and resources required for last-ditch captive breeding and reintroduction efforts. Such invasive, intensive recovery programs add many other management dimensions and require more adaptive and risky decisions.

Socially, at the national level, the American public was just becoming aware of the demise of a number of species but had not reacted sufficiently to spur government action to conserve even this last ferret population. At the local level, "business as usual" ranching practices continued to pursue complete eradication of prairie dogs because of their real and perceived competition with domestic livestock. There was little recognition of the ecological importance of prairie dogs and there were no incentive-based initiatives available to conserve this important resource. The lack of understanding and will to maintain viable prairie dog habitats for associated species was a marked failure.

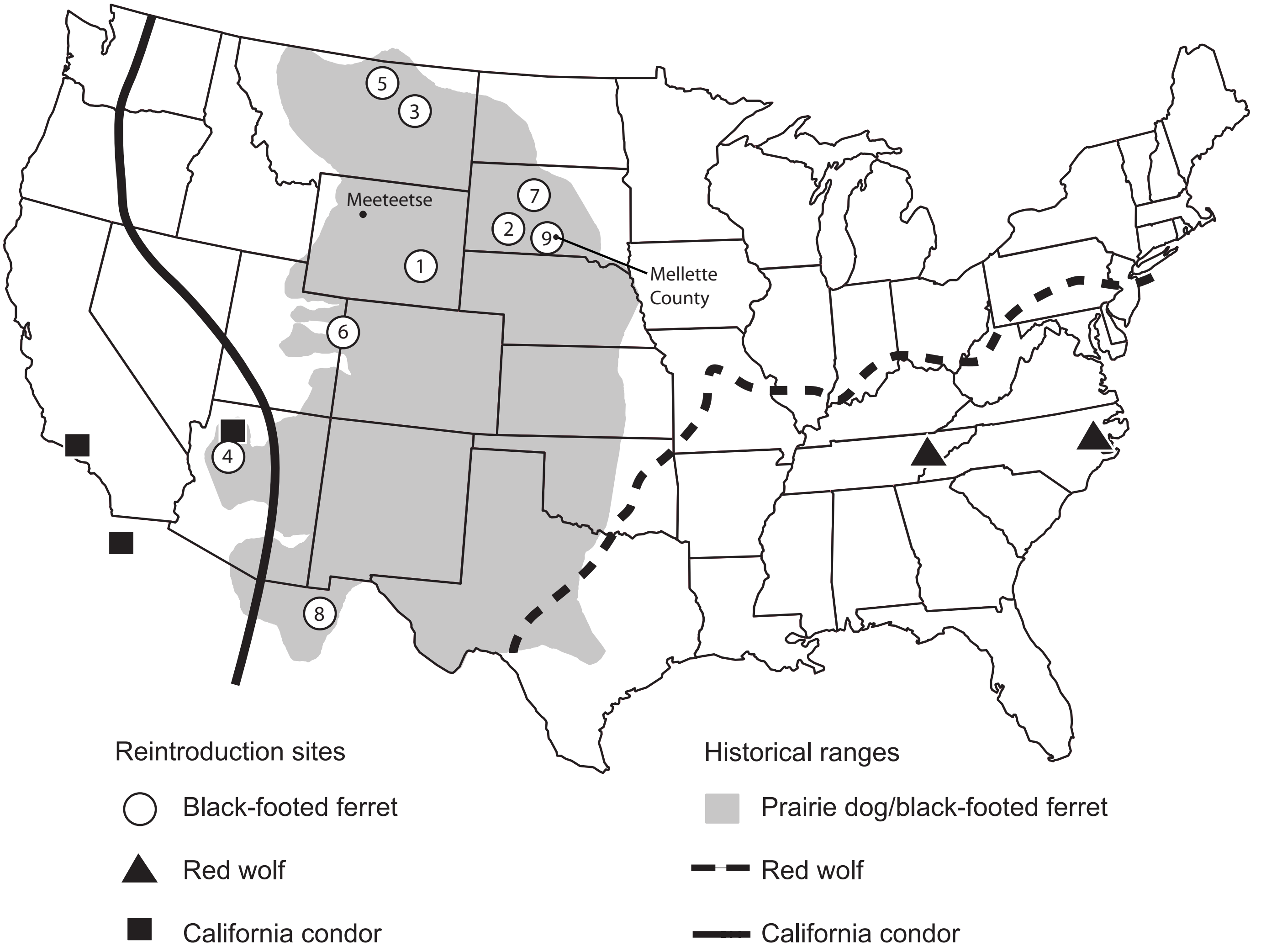


Figure 1. Location of black-footed ferret (*Mustela nigripes*) reintroduction sites overlaid on the collective ranges of three major prairie dog (*Cynomys*) species that are considered their obligate prey. Numbers represent the chronological sequence of ferret reintroductions. Also shown are locations of California condor (*Gymnogyps californianus*) and red wolf (*Canis rufus*) reintroduction sites in relation to their historical ranges.

Are we any more prepared today to deal with such a crisis in a nonregulatory manner? Are means to settle such diametrically opposed concerns readily available if similar circumstances occur again? Unfortunately, we believe the answer to these questions is “no” and reflects another substantial failure in the ability of divergent interest groups, State and Federal agencies, and tribes to find reasonable compromises needed to preserve sensitive species and biological diversity. The inability to find a single ferret in Mellette County, S. Dak., after 1974 was widely regarded at that time as the final demise of the species and must be viewed as a catastrophic conservation failure.

Despite unconfirmed reports, many biologists thought that ferrets were extinct until a ranch dog killed a wild ferret near Meeteetse, Wyo., in 1981. This event ushered in a long recovery process that was widely heralded as a remarkable second chance to conserve a species thought to be lost forever. Intensive attention was focused on this population of over 100 animals (20–40 adults). Considerable field data were acquired from 1981 to 1986 until epidemics of sylvatic plague and canine distemper took a heavy toll on both prairie dogs and ferrets. In hopes of salvaging the species, all remaining wild ferrets were removed from the Meeteetse population between 1985 and 1987 to initiate a captive breeding program.

It must also be acknowledged that underlying social support for endangered species conservation was just beginning to emerge in the 1960s and 1970s. Accordingly, no clear decisionmaking responsibilities were established for ferret recovery during this period, leading to later disputes and second guessing among involved entities. As a means of soliciting advice from experts and interested parties and to help prescribe management direction, WGFD established a Black-footed Ferret Advisory Team (BFAT) in 1982. Considerable acrimony existed within the recovery program during the 1980s and early 1990s, and, although it is never clear when criticism ceases to be constructive, we believe that more assertive and effective leadership by FWS during this period might have helped reduce conflict. We address this issue further in our Summary and Recommendations section.

Despite nearly two decades of extensive and intensive searches, and apart from occasional, unsubstantiated reports, no wild ferrets outside of reintroduction areas have been detected following capture of the last Meeteetse ferret in 1987. Further, we do not believe, given the passage of time and the expansion of plague in western environs, that any undiscovered ferret populations of wild origin exist anywhere in North America today.

With reduced size and quality of prairie dog complexes across most of North America and the presence of plague in many western States, the sustainability of reintroduced ferret populations has also been suspect until very recently. We believe that a wild, self-sustaining ferret population now exists at Conata Basin, S. Dak., and perhaps on Cheyenne River Sioux tribal lands in South Dakota and at Shirley Basin, Wyo. The ability to crop a harvestable surplus of ferret kits from Conata Basin for translocation to other reintroduction areas is a recovery program benchmark of exceptional importance. The Conata Basin ferret population likely represents the largest and most sustainable population that has existed since species listing in 1967, and perhaps for decades before.

Management of wild populations of ferrets (table 1) can be divided into three phases. In comparing these three phases, phase 1, from the mid-1960s to the mid-1970s in Mellette County, S. Dak., ended in disappointment and was greeted largely with resignation. Management efforts during that period were low in intensity and had few available resources. Phase 2, from 1981 to 1987 at Meeteetse, Wyo., was a catastrophe and was largely viewed as a second chance that nearly slipped away. Biological studies at Meeteetse enjoyed considerable resources and were much more intensive, but the existing recovery plan provided little realistic management guidance. Agencies responsible for ferret recovery at that time often disagreed on research and management needs, and required action was sometimes slow to develop. Phase 3, from about the year 2000 and into the future, has a much broader base of support, including a sustainable captive population and multiple reintroduction sites, yet presents new challenges such as habitat improvement needs, genetic management concerns, demographic supplementation in response to adverse stochastic events, diminishing financial resources, and so on. In short, the challenges of continued success now require anticipation of, and responses to, yet unidentified limitations in ferret recovery. Only time will tell whether program collaborators and resources will be adequate to address future uncertainties, but the organizational structure and depth of the recovery program partnership is a successful achievement in its own right and will perhaps ensure more effective responses to any forthcoming environmental or social obstacles.

Captive Breeding

A notable advance in black-footed ferret conservation was the capture in 1971 of six animals from the Mellette County, S. Dak., population for a landmark captive breeding trial. This action was deemed essential because, during the preceding 6 years of field studies in South Dakota, no other black-footed ferret population was discovered nor was any other population known to exist within the ferret's historical range. The 1972 captive breeding attempt was conducted at FWS's (now U.S. Geological Survey's) Patuxent Wildlife Research Center (Patuxent), where management preparations for captive breeding had begun in 1968 with breeding tests of surrogate species (domestic ferrets, *Mustela putorius furo*, and later Siberian polecats, *Mustela eversmannii*). Three additional South Dakota animals were captured and transported to Patuxent for captive breeding in 1972–73.

Efforts to breed black-footed ferrets at Patuxent were crippled from the outset by vaccine-induced canine distemper. Scientists at Patuxent were aware of the susceptibility of domestic ferrets to canine distemper and tested an attenuated distemper vaccine on domestic ferrets to determine safety and efficacy. Although the vaccine was proven safe in domestic ferrets, it induced fatal distemper in four of six vaccinated black-footed ferrets, demonstrating extreme susceptibility to this common viral disease.

Although only nine black-footed ferrets were available for breeding at Patuxent, four of which were lost to vaccine-induced canine distemper, the effort was modestly successful. Two litters of five kits each were born in successive years to a single female. Unfortunately, no kit survived more than a couple of days. The remaining captive ferrets eventually died, and, unfortunately, the breeding research program using surrogate animals was abandoned.

The Patuxent experience demonstrated that black-footed ferrets could be bred in captivity and that captive breeding might be successful if sufficient animals and resources were available. This experience also provided valuable lessons regarding diseases and endangered species recovery. Testing an attenuated vaccine on a surrogate species proved not to be the fail-safe procedure for ensuring vaccine safety for a highly susceptible, highly endangered species. Infectious diseases and their impacts on small populations became obligatory considerations for future recovery of ferrets and other endangered species.

Early ferret recovery efforts at Meeteetse were marred by poor planning, inadequate resources, conflict, controversy, and crisis. Events subsequent to discovery of the Meeteetse population have been, and will continue to be, used as both good and bad examples of endangered species management.

Table 1. Key events in recovery of the black-footed ferret (*Mustela nigripes*).

Year	Wild populations	Captive populations	Reintroduced populations
1964	Small wild population found in South Dakota		
1972		First captive breeding trials at Patuxent Wildlife Research Center, Laurel, Md.	
1974	South Dakota population extirpated		
1979		Last captive from South Dakota dies; species presumed extinct	
1981	Last known free-ranging population discovered near Meeteetse, Wyo.		
1986		First captive breeding effort using Wyoming stock	
1987	Last live ferret removed from Meeteetse; population extirpated	First successful reproduction and weaning in captivity	
1989		First of several additional captive breeding facilities established	
1991			First reintroduction: Shirley Basin, Wyo.
1994			Second and third reintroductions: Conata Basin/Badlands, S. Dak., and southern Phillips County, Mont.
1996			Fourth reintroduction: Aubrey Valley, Ariz.
1997			Fifth reintroduction: Fort Belknap, Mont.
1999		Captive population objective established in Species Survival Plan® reached; captive population considered stable	Sixth reintroduction: Colorado/Utah border
2000	First reintroduced population with harvestable surplus of kits for translocation to other sites		Seventh reintroduction: Cheyenne River Sioux tribal lands, South Dakota
2001			Eighth reintroduction: Janos, Chihuahua, Mexico
2002	Wild ferrets exceed captive ferrets in number		
2003			Ninth reintroduction: Rosebud Sioux tribal lands, South Dakota

Black-footed ferret recovery efforts in the 1980s and early 1990s were highly scrutinized and frequently criticized, often by individuals uninformed about recovery events and/or Federal and State laws regarding endangered species management. Although some reviewers and participants were well-intentioned and constructive, others ignored difficult problems and overlooked lessons learned in earlier ferret recovery efforts and other endangered species programs.

The Black-footed Ferret Recovery Plan of 1978 was written at a time when ferrets were thought to be extinct, and it provided little or no effective guidance for management of the Meeteetse population. In March 1982, WGFD quickly formed the aforementioned BFAT. This multiagency and private sector committee provided advice and guidance to WGFD in determining management direction for the Meeteetse population. Black-footed ferret numbers at Meeteetse increased from discovery in 1981 through 1984, when the population comprised approximately 40 adults and 90 juveniles. Based on this somewhat robust population and because no other wild population had been found (despite increased interest and improved search techniques), WGFD and FWS jointly decided in May 1985 to capture a small number of black-footed ferrets the following fall to begin a modest captive breeding trial. The WGFD's Sybille Wildlife Research and Conservation Education Center (Sybille) near Wheatland, Wyo., was selected as temporary quarters for captured ferrets. Ultimately, knowledge gained from Patuxent was used to develop technology and facilities at Sybille to support a long-term captive breeding program that would eventually provide animals for reintroduction and protect the species from extinction in the event of an unexpected catastrophe at Meeteetse.

The decision to initiate a captive breeding program did not come easily or without conflict. It took optimism generated by the high number of black-footed ferrets documented in the fall of 1984 and assurances that funding would be supplied by FWS in 1986 or 1987 for WGFD to commit to captive breeding. Although captive breeding was started less than 4 years after discovery of the Meeteetse population, in hindsight it should have been started earlier. The delay is understandable, however, and can be largely attributed to uncertainties in the availability of funding and suitable facilities and to the fear of animal loss and breeding failure. Lessons learned through this process were twofold: captive breeding of critically endangered species should be initiated early, and adequate advance planning and committed funding for personnel and facilities are essential. These lessons are not unique to the black-footed ferret program and were applicable to other endangered species, including the red wolf (*Canis rufus*) and California condor (*Gymnogyps californianus*).

The importance of these lessons became evident in the summer of 1985, even before the first attempts to capture ferrets for breeding. In June 1985, sylvatic plague was identified in Meeteetse prairie dog colonies. Sylvatic plague usually causes extensive die-offs in affected prairie dogs. In an attempt to halt the disease episode (by killing flea vectors of plague), FWS and WGFD conducted a massive plague-control program and dusted approximately 80,000 prairie dog burrows with the insecticide carbaryl. Nevertheless, the epizootic reduced Meeteetse prairie dog colonies by about 20 percent in the first year. Although the susceptibility of prairie dogs to sylvatic plague was well known, at that time black-footed ferrets were thought not to be susceptible. Siberian polecats, domestic ferrets, and other mustelids and carnivores are largely immune to sylvatic plague. Several years later, it was discovered that black-footed ferrets are actually exceptionally sensitive to plague. Black-footed ferret numbers at Meeteetse declined sharply over the summer of 1985, and only 58 animals were documented by August.

In September and October 1985, six ferrets were captured for captive breeding trials and moved into temporary quarters at Sybille. These captures led to discovery of another cause of the decline of ferret numbers at Meeteetse. One of the last two animals trapped died from canine distemper, an illness undoubtedly contracted before capture. Based on the experience at Patuxent with vaccine-induced canine distemper and the highly contagious nature of this disease, it was predicted that the remaining black-footed ferrets originally transferred to Sybille would succumb to the disease, which proved true. It was also predicted that most, if not all, animals in the free-ranging population at Meeteetse would be lost. Although extensive precautions had been taken to prevent introduction of diseases from outside sources, no precautions were taken to guard against known ferret diseases within the free-ranging colony. Another lesson learned.

At that point, management of the free-ranging black-footed ferret population and the fledgling captive breeding program were thrown into crisis. Given the reduced numbers of ferrets, it was unlikely that simultaneous efforts to maintain a wild population and start a captive breeding program would succeed; given the presence of disease, it was questionable whether a wild population could realistically be preserved. The WGFD, an agency accustomed to managing free-ranging wildlife, quickly, but with difficulty, decided to begin a second capture effort to obtain founders for captive breeding. This action was taken with recognition that it would likely lead to extirpation of the wild population. Interestingly, opposition to this second capture effort came primarily from individuals who disagreed with human interference and felt that black-footed ferrets should be allowed to go extinct.

In October and November 1985, six more ferrets were captured and placed in strict isolation quarters at the University of Wyoming until it was certain that all were free of canine distemper. Capture efforts were halted in late fall in the hope that any free-ranging black-footed ferrets remaining at Meeteetse would breed in the wild. Also during this period, WGFD invited the Conservation Breeding Specialist Group (CBSG) of the Species Survival Commission of the International Union for the Conservation of Nature and Natural Resources to provide expert advice on developing a captive breeding program.

Captive ferrets did not breed during the 1986 season, probably because of male immaturity and stresses associated with capture and a captive environment. Recovery partners experienced especially difficult times in 1985 and 1986. The responsible agencies received pointed and outspoken criticism; accusations ranged from allegations of mismanagement to intentional exposure of ferrets to canine distemper. Conflicting recommendations were received, including capturing all free-ranging black-footed ferrets immediately, removing captive animals from WGFD's care and terminating its role, curbing all further management intervention in the fate of the wild population, and so on. In spite of stresses, alliances between WGFD, FWS, and other recovery partners began to solidify.

Five free-ranging black-footed ferrets survived the canine distemper epizootic at Meeteetse, and two females subsequently produced litters in the spring of 1986. According to a contingency plan prepared by WGFD with assistance of CBSG and approved by FWS, the WGFD decided in August 1986 to capture all remaining animals. The last of 12 known wild black-footed ferrets was trapped in February 1987, and all captured ferrets were taken to a newly completed captive breeding facility at Sybille. The free-ranging black-footed ferret population at Meeteetse was thus extirpated, and the remaining captive individuals became one of the most endangered mammals in the world, as well as the last hope for the species. Survival and future recovery of the black-footed ferret now depended on development of an effective captive breeding program, which at that time had no proven track record.

Events from October 1981 through early 1987 occurred rapidly and developed in the absence of a current or applicable recovery plan, but critical decisions were still necessary. Perhaps issues faced by WGFD, FWS, BFAT, and CBSG could have been better anticipated and addressed, including analysis and consideration of probabilities of extinction of the small Meeteetse black-footed ferret population; when and how to best initiate captive breeding efforts; how to fund captive breeding; potential responses to epizootics of canine distemper and sylvatic plague; when and how to remove the last free-ranging animals to prevent extinction; appropriate responses to discovery of another wild ferret population; and advance identification and preparation of suitable reintroduction sites.

By spring of 1987, with funding assistance from FWS, the captive black-footed ferret colony was moved into permanent facilities at Sybille. With the assistance of CBSG and the University of Wyoming, WGFD improved captive husbandry protocols, began a genetic management plan, and began intensively monitoring black-footed ferret reproductive cycles and pairing events. Captive breeding techniques were developed with the intent of minimizing stress and injury and maximizing longevity, productivity, and genetic contribution of founder animals without promoting domestication. Two litters were born, and seven kits were weaned in 1987. Production of these kits was exceptionally significant, not because of the number of kits weaned or their genetic makeup but because it was finally demonstrated that black-footed ferrets could be bred and reared successfully in captivity.

The CBSG, WGFD, and FWS held a workshop on black-footed ferret conservation biology in 1986. A captive breeding program plan (*A Strategic Plan for the Management of Black-footed Ferrets in Wyoming*), with time-specific objectives, was written in 1987. This plan recognized that few animals were available for captive breeding and that many were related. It called for maintaining approximately 90 percent of the original genetic heterozygosity of founder ferrets over a relatively short period of 50 years. This would be accomplished by establishing a captive population of 500 animals with a stable age and sex distribution, which would provide an effective population of about 250 ferrets and approximately 200 breeding-age animals. During the early stages of the program, increasing the population had priority over managing genetics. Subsequently, ferret pairings were planned to maximize retention of founder alleles.

Another objective of the strategic plan was to raise enough animals to establish a second geographically removed population to protect the species from catastrophic loss. The two-facility objective was reached in 1988 when a few ferrets were moved from Sybille to the Henry Doorly Zoo, Omaha, Nebr., and the National Zoological Park's Conservation & Research Center, Front Royal, Va. Demographic and genetic data were maintained in a detailed studbook. Separate captive populations were genetically managed and bred as a single population. The strategic plan also called for initial ferret reintroductions to begin in 1991, provided that the captive population reached 500 animals with 200 breeding-age adults.

A revised Black-footed Ferret Recovery Plan was completed by FWS in 1988. It included most of the goals of the Wyoming strategic plan and called for ensuring immediate survival of black-footed ferrets by increasing the captive population to 200 breeding adults by 1991. Additionally, it included a downlisting goal of establishing a prebreeding population of 1,500 free-ranging, breeding-age ferrets in 10 or more populations, as widely distributed as possible over the historical range, by the year 2010.

Over the next few years, additional captive populations were established at the Cheyenne Mountain Zoo, Colorado Springs, Colo.; the Louisville Zoo, Louisville, Ky.; the Metropolitan Toronto Zoo, Toronto, Ontario, Canada; and the Phoenix Zoo, Phoenix, Ariz. The contribution of these zoos to ferret recovery was enormous. They received no monetary support from WGFD or FWS and initially were not allowed to use ferrets for exhibit. Another requirement was that participating zoos be accredited by the American Zoo and Aquarium Association (AZA), which had established a program to develop Species Survival Plans® to facilitate captive breeding of endangered and declining species. With growing involvement of AZA zoos and maturation of the captive breeding program in 1989, the technical advisory role previously filled by CBSG was vested in AZA through an established Black-footed Ferret Species Survival Plan (SSP) and associated Management Group of facility specialists.

The partnership between the AZA's SSP, WGFD, and FWS was, and remains, successful, and black-footed ferret recovery has benefited greatly from this relationship. Participants in the Black-footed Ferret SSP Management Group included representatives from involved zoos, WGFD, and FWS, as well as numerous outside advisors who provided extensive expertise in husbandry, veterinary care, disease, reproductive management, population management, and genetics. The commitment of the SSP Management Group, CBSG, and their many advisors was rewarded in 1991 when captive-bred black-footed ferrets were first reintroduced into the wild at Shirley Basin in central Wyoming.

With expansion of the reintroduction phase of black-footed ferret recovery to sites outside Wyoming, and with dwindling financial resources within WGFD, management responsibility for the Sybille captive breeding facility shifted to FWS in 1996. The breeding facility is now part of the National Black-footed Ferret Conservation Center and has moved to a new site in northern Colorado. The new facility became operational in the fall of 2005.

A review of the Black-footed Ferret Recovery Program, with particular attention to captive breeding elements, was undertaken by AZA in 1995, and a similar analysis and update was accomplished by CBSG in 2003. These critical reviews of the history, progress, and operations of captive breeding projects have been instrumental in evaluating problems and providing important input into the direction and management of captive breeding.

Beginning in 1997, an effort was undertaken to increase overall captive production and kit quality for reintroduction purposes. Ferrets excess to the SSP were used to develop limited field breeding projects in association with reintroduction efforts in Arizona, Colorado, and Montana. A separate field breeding facility (no accompanying reintroduction effort) was constructed near Raton, N. Mex., by the Turner Endangered Species Fund. Although many of the basic SSP husbandry and breeding procedures were employed, these projects were initially designed to test more hands-off breeding strategies in outdoor pens with well-developed prairie dog burrow systems. Breeding success at these facilities has been mixed and has varied substantially between sites. In addition, the expense of operating pen breeding facilities has often been greater than anticipated and, as a consequence, has affected other elements of reintroduction projects. The objective of increasing production and potentially improving the survival of released ferrets, however, remains a guiding principle of the recovery program and has been a recurring recommendation in all formal program reviews. Additional evaluation and refinements of pen breeding capabilities warrant further attention.

Although the black-footed ferret captive breeding program will continue to evolve, it has been a great success: the first animals were captured for captive breeding 4 years after discovery of the Meeteetse population; the program survived the sylvatic plague and canine distemper crisis of 1985 and extirpation of the species in the wild by 1987; and the first experimental reintroduction occurred just 6 years after the first animals were captured to initiate captive breeding. The captive breeding program has produced and weaned over 4,800 ferrets (through 2003) and has supported several reintroduction efforts across the former range of the species. In addition, the program has provided animals for essential disease and vaccine research, for survival enhancement, and for educational exhibit. For the foreseeable future, black-footed ferret recovery hinges on the continued success and management of the captive population by involved agency and zoo partners.

Reintroduction

With increasing success in black-footed ferret captive breeding efforts in the late 1980s, recovery program partners focused greater attention on restoring wild ferret populations. Initial interest was directed at reestablishing a ferret population at the site of their last wild origin near Meeteetse, Wyo., but sylvatic plague substantially reduced overall habitat quality on the Meeteetse prairie dog complex, thus rendering the site unsuitable for ferrets. Today, prairie dog populations in the Meeteetse area are still depressed, which highlights a serious obstacle to ferret recovery. In the absence of effective plague intervention and management capabilities, many affected prairie dog colonies may never regain historical population levels and may never support viable ferret populations. This issue is discussed at greater length below.

The primary goal of the black-footed ferret recovery program is to reestablish a sufficient number of viable, wild ferret populations in order to downlist and recover the species, remove it from ESA protections, and terminate the expensive captive breeding program now necessary to support species survival and recovery efforts. Between 1991 and 2003, 12 discrete reintroduction projects were initiated at nine reintroduction areas in six western States (Arizona, Colorado, Montana, South Dakota, Utah, and Wyoming) and at one site in northern Chihuahua, Mexico (fig. 1). The history and results of these specific reintroduction efforts are addressed elsewhere and will not be detailed here. Instead, we highlight overall direction, research, monitoring efforts, ferret survival, and success in general terms and from our personal views and recommended direction.

As of 2003, over 1,800 ferrets had been reintroduced into the wild. Success of these efforts, in terms of establishing self-sustaining populations, has been mixed and affected most significantly by habitat suitability (which, in turn, is most affected in recent years by the presence of sylvatic plague throughout most of the historical ranges of prairie dog species and ferrets). Only in South Dakota do large, relatively contiguous, and plague-free prairie dog complexes remain, and the greatest reintroduction success to date has been at the Conata Basin site (Buffalo Gap National Grasslands) in south-central South Dakota. Conata Basin experienced exponential growth in the wild ferret population following only 3 years of reintroduction and a total release of 165 captive animals. Ferrets at Conata Basin may have spread through most of the available habitat and are possibly approaching population saturation levels, having produced a relatively consistent 60 to 70 litters annually over the past 3 years. Conata Basin is the only site to have reached a success level that allows translocation of wild-born kits to other reintroduction sites, and kits from Conata Basin have been used to support reintroductions in Colorado and at two other sites in South Dakota. Similar successes are expected at two more recent South Dakota reintroduction sites that also support relatively large, plague-free prairie dog complexes (Cheyenne River Sioux and Rosebud Sioux tribal lands). In contrast, plague has been documented either in or around five of the other reintroduction areas outside of South Dakota.

To date, there have been six reintroduction projects in black-tailed prairie dog habitat (Montana, Mexico, and South Dakota), two in white-tailed prairie dog complexes (central Wyoming and an area straddling the Colorado/Utah border), and one in Gunnison's prairie dog habitat (northwestern Arizona). Differences in prairie dog colony size, density, and life history (e.g., hibernation) exist both between and within species (over the extent of each species' range) and undoubtedly influence site quality and success of ferret reestablishment. For the most part, black-tailed prairie dogs currently occupy definable "towns" of varying size (but historically included enormous colonies), exist at greater densities, and typically do not undergo extended torpor. On the other hand, Gunnison's and white-tailed prairie dogs are more scattered and less dense over areas they occupy and hibernate for extended periods.

Other regional factors such as geography, vegetation, annual precipitation, and drought also affect site suitability and reintroduction potential. Land ownership patterns, land use, access, and vehicle use constraints further affect implementation and monitoring efficacy of reintroduction projects. As a consequence of such dynamics, the recovery program has experienced both outstanding and rapid reintroduction success, as well as projects that have struggled to maintain even minimal populations. Still, no reintroduction project is regarded as a failure, and all have provided vital experience and information to help foster ongoing and future recovery efforts across the ferret's historical range. Moreover, given the severe limitations in available reintroduction sites in North America today, it would be imprudent to give up on any reintroduction area that has the necessary land base and potential for improved habitat conditions and ferret recovery.

Only ferrets considered excess to the captive population have been used to support reintroduction projects. The captive, SSP population is regarded as the essential foundation of the species today. And with the exception of ferret releases in Mexico, all reintroductions have been accomplished under a special provision of the ESA (section 10(j)) that provides for designation of reintroduced populations as "nonessential, experimental." Ferrets released into nonessential, experimental population areas (as established via Federal rulemaking and ESA consultation procedures) are no longer classified or managed as endangered but are given protection and management flexibility similar to that provided for "candidate" species (candidates for listing under ESA but not yet listed). This relaxed management flexibility was necessary to gain the support of State governments and private landowners for releases of an endangered species into areas with fragmented ownership patterns of public and private lands.

The section 10(j) nonessential, experimental provisions facilitated ferret reintroduction trials; it is unlikely that most projects would have been successfully implemented without 10(j) or a similar mechanism to reduce the perceived consequences of potential expansion of endangered ferrets onto private lands. The nonessential, experimental designation has other limitations that impede ferret recovery, however, and a review of the utility of 10(j) and reexamination of other options to tailor reintroductions to site-specific situations are warranted. More discussion is provided below.

With the recovery program becoming more focused on reestablishing wild ferret populations in the early to mid-1990s, other forms of partner acrimony began to surface. Disputes over "soft" versus "hard" release techniques, ferret preconditioning and predator avoidance training, predator control, use of radio telemetry to document survival, how and where to prioritize excess ferrets for release, State versus Federal authorities, and other research issues, some of which first began to surface during the Meeteetse era, seemed to deepen divisions among some participants.

Despite individual and agency conflicts and occasional setbacks, a committed partnership of biologists and administrators set aside differences (or, perhaps more accurately, worked around them) to focus attention on biological and social impediments to ferret recovery. As a consequence, reintroduction efforts continued to gather momentum between 1991 and 2003, and a wealth of information was gathered over that period about how to effectively reestablish ferret populations and respond to obstacles.

Also, the recovery program experienced a somewhat unexpected and positive turnaround in the status of two reintroductions over the past several years. Reintroductions at Shirley Basin, Wyo., were suspended in 1994 because of an extensive plague outbreak. Subsequent monitoring suggested that the small remaining ferret population was likely to be lost by the end of the 1990s; however, starting in 2002, the Shirley Basin population exhibited its own exponential growth and appears to be rapidly developing into a self-sustaining population. Prairie dog populations in Shirley Basin are also rebounding. Likewise, wild ferret production at Aubrey Valley in northwestern Arizona has recently increased following years of reintroduction attempts, probably as a result of spring ferret releases (releases designed to place ferrets in the wild when they can best exploit prairie dogs emerging from hibernation and young pups).

Perhaps one of the most significant findings from the early reintroduction development stages was recognition of the importance of preconditioning captive ferrets prior to release in the wild and an associated partner commitment to expand preconditioning capacity by constructing a number of outdoor facilities at or near reintroduction sites in Arizona, Colorado, Montana, New Mexico, and South Dakota. In simplest terms, preconditioning is the exposure of captive-produced ferrets to a more natural outdoor environment with relatively large pens, prairie dog burrow systems, and live prairie dog prey. In these pens, cage-reared ferrets become accustomed to the security and life needs of prairie dog colonies; essentially, they learn to behave like wild ferrets. As addressed above, outdoor pen facilities in Arizona, Colorado, Montana, and New Mexico were also used to conduct experimental breeding trials to increase the number of animals available for reintroduction.

Certainly, much has been learned about reintroducing ferrets. Still, many pressing uncertainties remain, particularly those dealing with management of ferrets in plague-affected environs, and additional research and reintroduction trials are warranted. And perhaps one of the best ways to speed recovery is to “cast a wide net” by placing ferrets in as many potential sites as possible and letting ferrets ultimately reveal what constitutes favorable habitat and management conditions.

As noted above, in 1995 the AZA was contracted by FWS to conduct a comprehensive review of the ferret recovery program. In this review, the AZA examined the status and success of captive breeding and reintroductions, as well as the administration and general decisionmaking procedures of the program. Much of the information was gathered through a series of partner workshops. A final report to FWS in 1996 included many valuable and specific recommendations on the biological and administrative needs of the recovery program. With waning funding in WGFD and expanding recovery efforts beyond the State of Wyoming, in 1996 FWS assumed primary responsibility for operation of the Sybille breeding facility and management of captive and field recovery activities. Following guidance provided in the AZA report and as set forth in ESA, FWS also established the Black-footed Ferret Recovery Implementation Team (BFFRIT) in 1996 and invited participation of agencies, organizations, and tribes directly involved in ferret recovery activities.

The BFFRIT replaced the original BFAT and subsequent Interstate Coordinating Committee as the vehicle for maintaining partner coordination and input into recovery program direction. The BFFRIT is composed of 26 cooperating State and Federal wildlife and land management agencies, tribes, zoos, conservation organizations, and the National University of Mexico. The BFFRIT charter established the Executive Committee (administrators of agencies/organizations who address recovery program policy and funding issues), the Conservation Subcommittee (composed of technical experts to deal with field reintroduction and research elements), and the Education Outreach Subcommittee (to expand public awareness of the recovery program and help pursue outside funding opportunities). The SSP Management Group, established originally by the AZA in 1991 and made up principally of zoo representatives, also effectively serves as a technical subcommittee to the BFFRIT and provides input and expertise on management of captive breeding programs.

Although FWS retains ultimate authority, the BFFRIT provides essential input and recommendations on all matters related to ferret recovery and has effectively guided program direction since its inception. To establish more balanced and objective procedures for allocating ferrets for reintroduction and research purposes, FWS (through the BFFRIT) also developed an annual ferret allocation and project evaluation process in 1996. This allocation process sets priorities for ferret distribution based on the biological suitability of proposed release sites, overall project and/or research merit, and potential recovery program benefits. Allocation proposals, which provide details on habitat attributes of project areas, disease and predator presence and management capabilities, project/research design and implementation capabilities, and so on, are submitted to FWS by mid-March each year. The proposals are then distributed to BFFRIT members for review.

The FWS awards a preliminary ferret allocation in late May via a report that fully discloses (albeit anonymously) comments and recommendations provided by BFFRIT members and a justification of FWS findings. The number of ferrets identified in the preliminary allocation is determined from an expected production level based on a 5-year average recruitment rate from the number and age distribution of female ferrets presently in the SSP-managed population. For now, and into the foreseeable future, first priority for ferrets goes to SSP facilities to maintain the genetic representation and viability of the essential captive population. Final allocation decisions are made in late summer and depend on the actual production achieved by SSP facilities and field breeding projects, as well as on resolution of any permitting or other project implementation deficiencies (e.g., funding, partnership commitments).

The current organizational structure of the Black-footed Ferret Recovery Program has had the benefit of time, conflict, and critical analysis to evolve. Fortunately, ferrets have persisted during periods of unforeseen crises and human mistakes. The BFFRIT is a product of important lessons learned over the history of the ferret program, and we believe it offers a good example of an effective strategy for management of large, complex, endangered species recovery programs. Instead of a typical, more academically based and smaller recovery team, a recovery implementation team provides a transparent decision process and equal voice to a large number of involved agencies, tribes, and organizations. Although FWS retains ultimate authority and responsibilities as specified in the ESA, the BFFRIT is relied on to help make informed program decisions, help resolve partner disagreements and other program conflicts, and generally keep recovery efforts moving in a positive direction. We regard such continued partner participation as essential to successful recovery of the black-footed ferret.

Finally, the most pressing limitation to ferret recovery is availability of suitable habitat to restore and support wild populations. Although program partners have always understood that habitat availability is key to recovery, other program imperatives between 1985 and 1997 (i.e., development of captive breeding and reintroduction capabilities) somewhat diluted focus on habitat issues. In 1998, the BFFRIT Conservation Subcommittee was tasked to identify and prioritize the top 10 sites that could support ferret reintroduction across North America, as well as secondary areas that could possibly be developed into additional reintroduction sites. In 1988, only 10 years earlier, an internal FWS document suggested that as many as 38 suitable ferret reintroduction areas existed in the United States. That document was based solely on suggestions from program partners and did not attempt to accurately assess current prairie dog populations, complex size and quality, the status of plague, or other practical biological and political factors (e.g., land ownership patterns) necessary to determine reintroduction potential.

With more detailed surveys of BFFRIT partners, the 1998 assessment of site potential indicated that only nine sites could immediately support ferret reintroductions across North America. Five of these sites were already engaged in reintroduction projects, and three more were activated between 1998 and 2003. Since 1998, a few other potential release areas have been identified, but it is clear that prairie dog habitat throughout the historical range of the ferret has been so severely degraded that ferret recovery is not feasible without restoration of large, healthy prairie dog complexes.

What constitutes a suitable prairie dog complex for ferrets is a question still under scrutiny by program partners and is a pertinent issue to be addressed in an upcoming and long overdue revision of the Black-footed Ferret Recovery Plan. In examining the results of reintroduction efforts to date, the only relatively large, self-sustaining, wild population of ferrets (ca. 250–400 animals) is at Conata Basin, a site that contains some 6,070 ha of closely distributed and relatively dense black-tailed prairie dog colonies—prairie dog colonies that are also free of sylvatic plague and are managed to preserve high prairie dog habitat values. Although prairie dogs of all three species are well dispersed throughout their former ranges, prairie dog complexes are very small and highly fragmented compared to historical conditions. There are very few places within North America that approximate the quality of habitat for ferret recovery exhibited at Conata Basin.

The revised Black-footed Ferret Recovery Plan (published by FWS in 1988) sets forth a downlisting objective by the year 2010 of 1,500 adult (breeding) ferrets, established in no less than 10 separate populations across the historical range of the ferret, with at least 30 individuals in each population. Although a prebreeding census of 1,500 adult ferrets may be attainable with continued recovery success in the few large prairie dog complexes that exist, there appear to be only four or five sites today that have the potential to support viable ferret populations, the majority of which will likely be in plague-free complexes in South Dakota.

Future recovery of the black-footed ferret hinges on our ability to successfully reintroduce and reestablish relatively large, healthy populations in the wild. Unlike two other endangered, high-profile carnivores of the West, the gray wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*), the entire breadth of habitat within the ferret's historical range has been materially impacted: there are few large expanses of Federal public land with sufficient prairie dog habitat to support black-footed ferret populations at the present time. Furthermore, although the amount of land potentially available for habitat restoration across the historical range of the ferret far exceeds potential capabilities for two other critically endangered species, the California condor and red wolf (fig. 1), there are significant social and political impediments to restoring and managing large blocks of grasslands for prairie dogs and ferrets. Prairie dogs are still largely regarded as vermin by private landowners and agricultural interests, and only small, relatively fragmented complexes are typically tolerated, if at all.

And so, ironically, we appear to be at yet another important crossroad for this species. Having brought the ferret back from the brink of extinction, having invested enormous national resources to right an ecological wrong, and having developed the necessary capabilities and expertise to actually recover this species, the future of the ferret hangs on our social and political will to set aside and develop sufficient habitats that could be managed for prairie dogs, ferrets, and other sensitive prairie wildlife species. Ferret recovery efforts have come full circle, and it will be an enormous challenge to overcome a prevailing attitude of “not in my backyard” when so few suitable, welcoming backyards are presently available.

Summary and Recommendations

Given the status of the ferret in 1987, when only 18 live animals remained, we submit that ferret recovery has been one of the most successful endangered species programs to occur anywhere, at any time. Table 2 compares several recovery parameters for three well-known North American species that were listed as endangered in 1967. The black-footed ferret, California condor, and red wolf are notable “grandfathered species” that have always been included in the various versions of ESA. Each became further imperiled after listing, and each was subsequently removed from the wild for captive breeding and eventual reintroduction. Figure 1 indicates the historical range of these species and the sites where reintroduction has occurred. Clearly, the “recovery glass” is potentially “half full” for the ferret compared to species that mature less quickly, have fewer young, and whose range and essential habitats have been even more drastically altered.

The lessons taught by ferrets, condors, and red wolves should be carefully heeded. Reducing any species to such critically low population levels that captive breeding becomes the only possible recovery strategy is a poor way to ensure persistence, much less recovery. Extinction risks are elevated, recovery becomes more expensive, and bringing species into captivity may remove assurances that adequate habitats will be available for later reintroduction.

Table 2. Comparisons of some recovery parameters for three North American endangered species removed from the wild, propagated in captivity, and reintroduced into their historical ranges, 1967–2003.

	Black-footed ferret (*Mustela nigripes*)	**California condor (*Gymnogyps californianus*)**	**Red wolf (*Canis lupus*)**
Year species listed	1967	1967	1967
Year extinct in wild	1987	1987	1980
Number removed from wild	18	27	17
Initial number used in breeding	7	14	14
Number propagated in captivity to date	4,800+	283	727
Number held in captivity, breeding	~400	130	300
Year reintroduction began	1991	1992	1987
Number reintroduced to date	~1,800	~167	~120
Number of attempted reintroduction sites	9	7	2
Number weaned or fledged in wild	~1,200	1	289
Number in wild	~600	~80	~100
Reintroduction sites, likely viable	3	0	1
Reintroduction sites, not viable	2	0	1
Reintroduction sites, unknown viability	4	7	0

The ferret recovery program has experienced a number of successes, failures, and hard-learned lessons over the years. It is important to continually characterize progress so the direction and speed of recovery can be adjusted accordingly. Overall, we believe that the ferret recovery program will probably continue to be successful, despite many near disasters and remaining obstacles. Ferret recovery efforts may be compared internally by contrasting results of different activities over time. Comparisons of the progress and success of other endangered species recovery efforts may also provide perspective that will aid ferret recovery.

To date, we believe that (1) black-footed ferret captive breeding has been highly successful, (2) ferret reintroductions have achieved a low to moderate degree of success, and (3) wild population management has experienced a low degree of success. Marked improvements and efficiencies have occurred in all of these areas over the last decade, however.

The most notable success of captive breeding has been the creation of a mutually supportive network of staff and facilities that successfully raise animals in a protected environment to ensure species survival and provide animals for reestablishment of wild populations. Problems that have occurred in this recovery component have been straightforwardly addressed. One nagging limitation that may or may not be possible to fully overcome in a captive environment is the relatively low whelping success in females (as compared with wild whelping rates). The most important lesson learned over the course of the ferret program, however, is that biological breakthroughs in complex recovery efforts can only be realized via the successful involvement of many diverse partners.

Ferret captive breeding may become more efficient as limitations are identified and addressed, but this recovery component is mature, with over 15 years of accumulated experience. Most attainable internal refinements may already have been achieved. If increased numbers of animals are required for reintroduction, it may be most practical simply to increase the number or size of facilities. Captive breeding of ferrets is a tightly controlled process with few extraneous factors affecting its continued success or failure. Extended captivity may reveal future biological constraints (e.g., inbreeding suppression), but most political and social obstacles to captive breeding appear to have been adequately addressed.

At present, the knowledge and resources needed for continued success of the captive breeding program appear to be in place. Nevertheless, we recommend that continued and rededicated attention to partner coordination and involvement be nurtured through the SSP Management Group and BFFRIT. Although this recommendation may appear gratuitous given present successes, renewed emphasis is essential to address a crucial, laborious, and continuing program element whose failure would undercut all other recovery activities. A recurring error of many recovery efforts is to gradually pay less attention to successful foundation components when new limiting factors are identified.

Likewise, progress in reintroducing ferrets and establishing viable, wild populations requires continued nurturing of program cooperators and development of new partnerships with other States across the ferret's historical range. The most notable success of the reintroduction component has been the relatively rapid involvement of the few suitable sites for active releases, but few large, high-quality prairie dog complexes remain, and future recovery depends on both short-term and long-term habitat restoration. In concert with renewed efforts to identify and enhance potential recovery habitat, new reintroduction trials and continuing research to refine vaccines and develop other possible disease management capabilities are also essential.

The most notable accomplishment of wild population management has been the apparent sustainability of at least one reintroduced population. The ferret population at Conata Basin, S. Dak., is believed resilient enough to withstand harvest of surplus animals for translocation to other reintroduction sites. This is a remarkable accomplishment and indicates a population likely more stable than any other extant population during the last half century.

The review of the Black-footed Ferret Recovery Program by CBSG in June 2003 and the subsequent report issued by CBSG in January 2004 provided many practical recommendations to further ferret recovery and addressed issues and program needs related to captive breeding, reintroduction, disease, and habitat. Many of our views and recommendations echo information contained in the CBSG report; however, given the current status of the recovery program, after almost 20 years of captive "life support" for the ferret, and the prospect of a difficult recovery future (given habitat limitations), perhaps other, more fundamental questions need to be asked and other key recovery priorities more fully pursued.

To realistically fulfill our recovery mission, how do we secure greater commitments for financial resources, private land incentives, and public land-use reforms necessary to set aside, develop, and sustain sufficient habitats across the historical range of the ferret?

Given the presence of plague in the environment and the timetable likely necessary to restore suitable prairie dog complexes, a foundation of available sites needs to be identified and attendant implementation strategies and schedules prescribed in a timely manner. It may take 10–20 years of intensive management to enhance complexes of prairie dog habitat to the point that they can support healthy ferret populations; planning and commitments must start soon. Federal public lands (national grasslands, Bureau of Land Management property, national wildlife refuges, national parks and monuments, and military lands) should bear a disproportionate amount of habitat development. Responsibilities under section 7(a)(1) of the ESA (a provision requiring all Federal agencies to fully promote and support endangered species recovery) should be reinforced at the national level, both with funding and refocused priority, to establish and manage large prairie dog complexes wherever possible. Partnerships with tribes and private land owners must be pursued to secure recovery areas over those portions of the ferret's historical range where public lands are largely absent. Cooperative efforts with Canada and Mexico should continue in order to develop recovery sites at the northern and southern extents of the ferret's historical range.

How can administrative procedures be improved to more effectively and rapidly develop suitable black-footed ferret reintroduction areas and secure long-range management assurances necessary to perpetuate viable, wild populations?

All ferret reintroductions in the United States have been accomplished under ESA section 10(j) provisions, which relax many of the strict prohibitions of the ESA. Section 10(j) has been an important management tool and was necessary for initial ferret reintroduction efforts. Nevertheless, 10(j) also has limitations and liabilities. Despite successful development of ferret reintroduction projects over most of the best remaining habitats in the United States since 1991, the administrative processes required to establish 10(j) experimental population sites typically require 2 years to complete and considerable investments of staff and funding. It is not a provision that allows rapid response to new opportunities. More importantly, 10(j) is somewhat one-sided in effect and does not provide long-range assurances of support by affected parties. It can hinder implementation of program changes in response to identified needs and has been used by involved agencies to justify positions of social and political expediency rather than to fulfill conservation obligations. Other than reducing political opposition to initial reintroduction efforts, 10(j) has done little to assure reestablishment of ferrets.

Still, we do not advocate stronger regulations or constraints to guide ferret recovery; indeed, we suggest the opposite. The time to be most careful and restrictive with species like the ferret, condor, and red wolf is when they are declining, so as to keep them from slipping into such a precarious abyss in the first place. A process is needed through which responsible agencies are given sufficient resources and broader latitude to quickly develop site-specific strategies that define the boundaries of proposed recovery areas, prescribe the scope of agreements, and, like 10(j), hold no private parties accountable for uses or development of their property that might result in inadvertent losses of endangered ferrets. The ferret program needs to become even more proactive and not shy away from potential risks of individual project failure and animal losses. Again, we need to cast a wide net while reducing the fear of repercussions and impacts to private property that accompany efforts to recover endangered species.

How can resources allocated to endangered species recovery at the national level be better prioritized and distributed to address biological imperatives?

The manner in which endangered species program priorities are established and funded warrants review. Although we certainly support other programs and efforts to recover endangered species, overall national priorities should be biologically based and focused on those species in greatest peril and for which habitat protection would have the greatest overall ecological benefit. Black-footed ferret recovery has achieved some remarkable successes despite a history of inadequate funding. Increased funding could have substantially accelerated species recovery, focused greater attention on critical program elements such as habitat conservation and restoration and expanded partnerships, and perhaps would have helped avoid some of the pitfalls encountered.

Enormous resources have been poured into recovery efforts for the gray wolf and grizzly bear in the Rocky Mountain region with great success and public benefits, but these species enjoy stable habitats over significant portions of their historical ranges—habitats that support large, nonthreatened populations to the north. The black-footed ferret has no comparable safety net of extant population reservoirs. Moreover, the grassland/steppe ecosystem upon which the ferret depends is imminently more threatened, and its loss would have far-reaching consequences to a host of other native plant and wildlife species.

We recognize that these questions and suggestions address larger issues of regulation, policy, and current management direction and practices for numerous State and Federal agencies. We also understand that there are no easy fixes and that change may be slow in coming. Still, what better example of a species recovery program could be used as a springboard to critically review functional elements of ESA, interagency coordination and management needs, partnership capabilities, and administrative processes needed to secure greater habitat stability and foster species recovery? These questions and issues are in need of more focused scrutiny and attention by FWS, partner agencies, organizations, and tribes of the BFFRIT and other endangered species programs.

Acknowledgments

General data on red wolf and California condor used in this paper were obtained from FWS recovery program staff. The interpretation and analyses of those data presented here are our own.

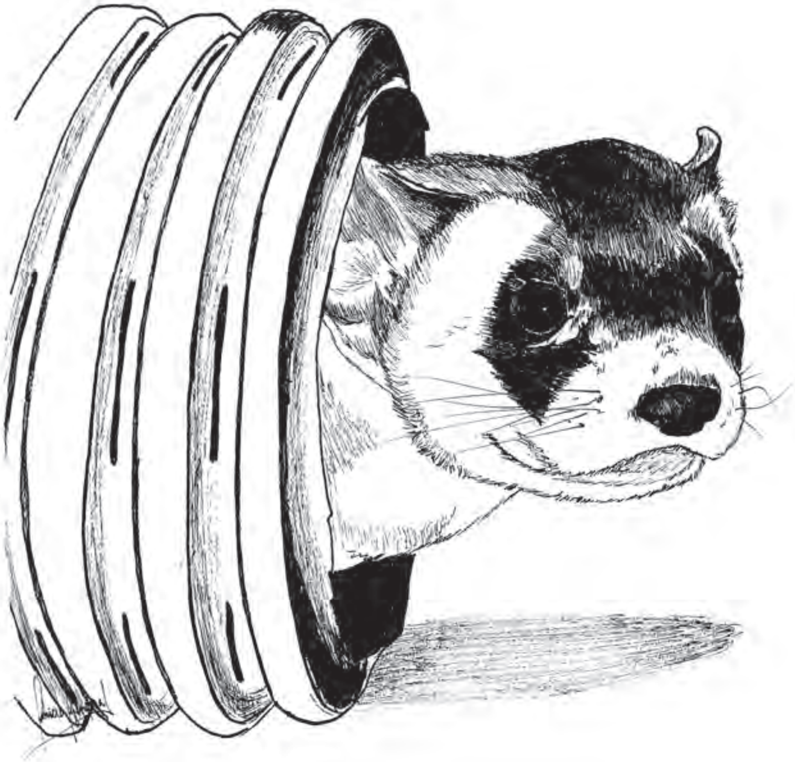
Recovery Plans and Recovery Program Analysis Reports

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management planning workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

Hutchins, M., Wiese, R.J., and Bowdoin, J., 1996, Black-footed ferret recovery program analysis and action plan: Bethesda, Md., American Zoo and Aquarium Association, 137 p.

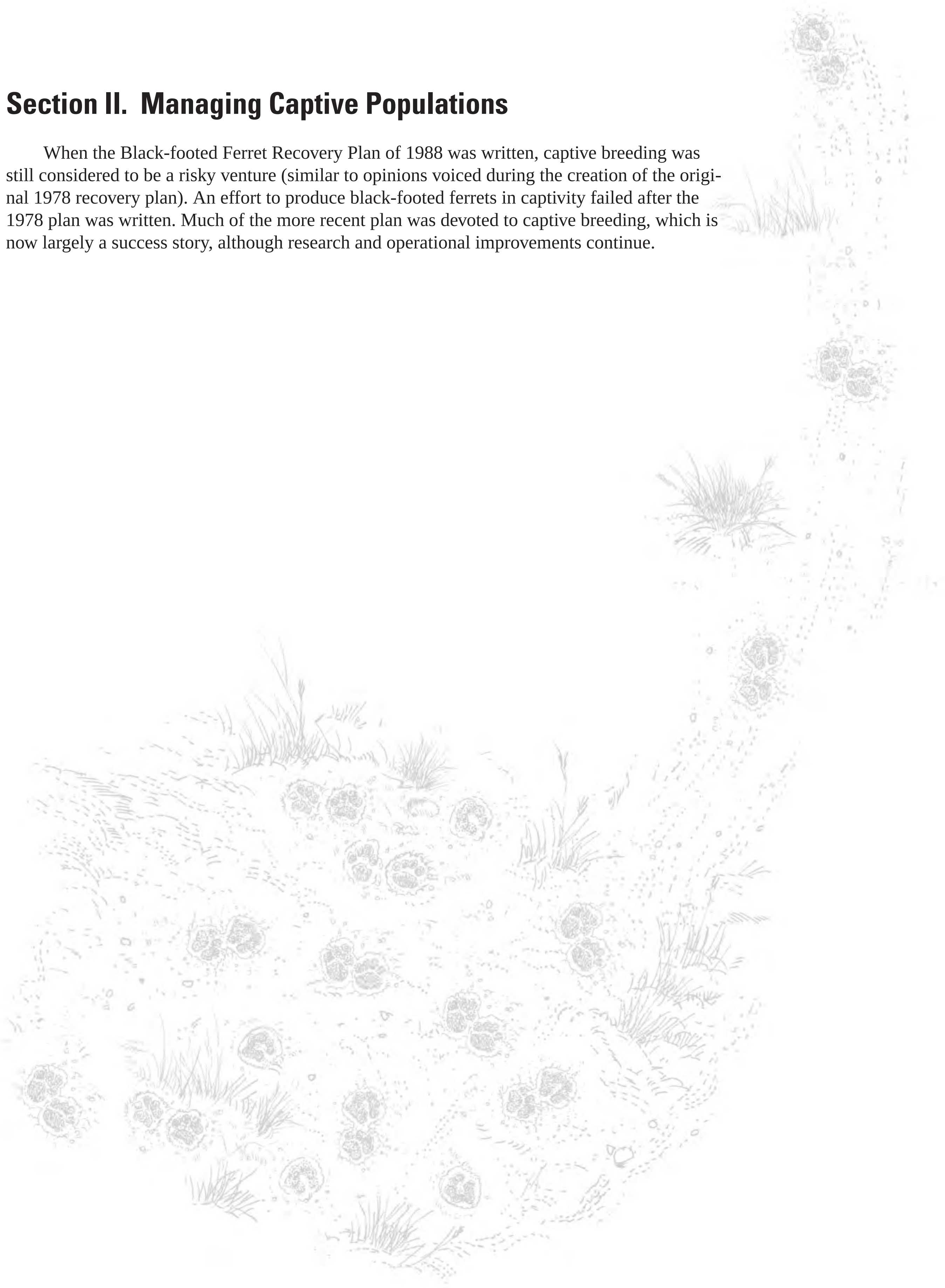
U.S. Fish and Wildlife Service, 1978, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 145 p.

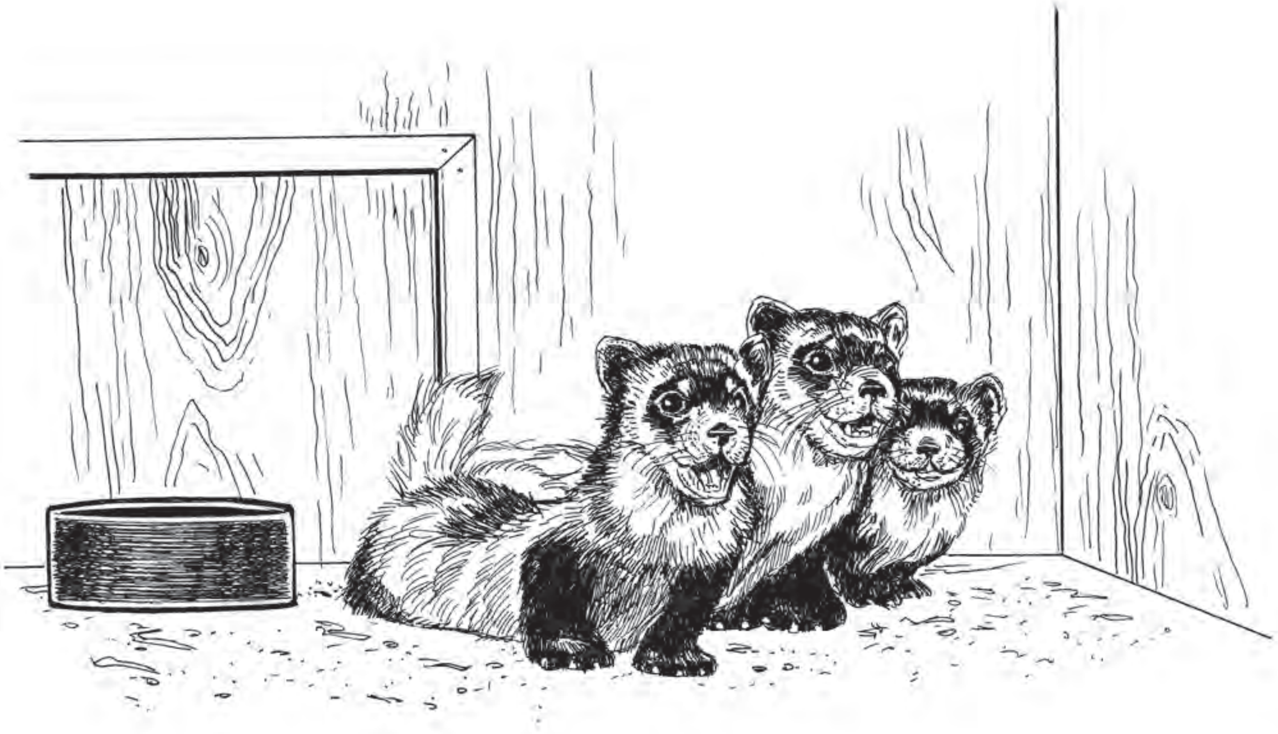
U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.



Section II. Managing Captive Populations

When the Black-footed Ferret Recovery Plan of 1988 was written, captive breeding was still considered to be a risky venture (similar to opinions voiced during the creation of the original 1978 recovery plan). An effort to produce black-footed ferrets in captivity failed after the 1978 plan was written. Much of the more recent plan was devoted to captive breeding, which is now largely a success story, although research and operational improvements continue.





An Adaptive Management Approach for Black-footed Ferrets in Captivity

By Paul E. Marinari[1] and Julie S. Kreeger[1]

Abstract

Management of black-footed ferrets (*Mustela nigripes*) in captivity has historically utilized a flexible, adaptive approach as additional information about the species is obtained. Increased survivorship at reintroduction sites within the ferret's historical range has further allowed innovative approaches to animal husbandry. Ferret recovery has benefited from changes in breeding schemes, nutrition, and vaccinations. Production of kits increased when animals were paired during daytime hours and allowed to remain together for 3 consecutive days. The Toronto Zoo Small Carnivore Diet was found to be a well-balanced, cost-effective, nutritious food for ferret maintenance and reproduction. PureVax® Ferret Distemper Vaccine provided protective titers under a variety of management scenarios. Changing program needs and flexibility in animal management are assessed yearly in order to balance maintenance of genetic diversity with maximum productivity.

Keywords: adaptive management, black-footed ferret, breeding, captive, *Mustela nigripes*, nutrition, reproduction, vaccination

Introduction

Captive management of endangered species requires an adaptive approach, incorporating new information relevant to changing program goals while ensuring quality animal care. Additionally, a system of checks and balances is needed to ensure that changes in management do not adversely affect either animal health or the primary goals of captive breeding—productivity and maintenance of genetic diversity. The fate of the black-footed ferret (*Mustela nigripes*) was placed in the hands of captive breeding efforts in the late 1980s when a decline of the last known wild population was identified. The decline of this population, located near Meeteetse, Wyo., led to the capture of 18 individuals of the species and was the start of a complex, multipartner recovery effort, which is conducted under the auspices of the American Zoo and Aquarium Association's Species Survival Plan® (SSP) program and is guided by the Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) and a manual of husbandry techniques (Lyster and others, 2002).

One of the primary goals identified in the Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) involves development and maintenance of a large, stable, and genetically managed captive breeding population, which has been further defined as a core breeding population of 240 adults (90 males, 150 females) located in six geographically separated facilities. Facilities currently housing captive breeding populations include the U.S. Fish and Wildlife Service's (FWS) National Black-footed Ferret Conservation Center (Center) in Wellington, Colo., (originally managed by the Wyoming Game and Fish Department and later the FWS at Wheatland, Wyo.), the Smithsonian National Zoological Park's Conservation & Research Center (Virginia), the Louisville Zoo (Kentucky), the Cheyenne Mountain Zoo (Colorado), the Toronto Zoo (Ontario, Canada), and the Phoenix Zoo (Arizona).

At the outset of the captive breeding program, all facilities tried to follow identical animal husbandry and management protocols based on the initial success of the Wyoming Game and Fish Department's (WGFD) program. Since 1987, this has led to the production of over 5,100 black-footed ferret kits through natural breeding and assisted reproductive technology. During this time, much has been learned about ferret behavior, reproductive technology, nutrition, and other factors associated with animal husbandry and captive colony maintenance. The ability to experiment with different management schemes in the ferret program has been key to these achievements. In the mid-1990s, the FWS assumed operational oversight of the largest ferret colony, which is located at the Center. The Center houses approximately 55 percent of the world's captive black-footed ferrets and serves as the hub for all ferret-related activities. Given the large population of ferrets housed there, the Center is an ideal place to implement a flexible and adaptive approach in all areas of black-footed ferret captive management. Additionally, the Center staff works both independently and in collaboration with research-

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ers to investigate questions concerning reproduction, nutrition, disease, and genetics as they relate to captive breeding.

Many changes have been incorporated into the captive breeding program based on studies addressing factors that affect the number of kits produced and weaned (defined as kits surviving to 90 days of age). This paper reviews three areas of management that have been addressed through studies at the Center: breeding strategies, nutrition, and vaccination against disease.

Breeding Strategies

A primary goal of the SSP is to optimize genetic management of the captive population (Ballou, 1984; Russell and others, 1994; Miller and others, 1996) by maintaining 80 percent of the genetic diversity present in the founder population for the next 25 years. Since only 7 of the original 18 animals successfully reproduced, genetic diversity has been limited from the outset. Males and females are paired utilizing the mean kinship and inbreeding coefficient strategy (Ballou and Oakleaf, 1989). This strategy identifies several potential males for each female in the SSP breeding population. Efforts to equalize founder representation are succeeding (Wisely, 2001), indicating that the mean kinship and inbreeding coefficient strategy is an appropriate tool for managing the captive population.

Prior to 1996, all ferrets at the Center, as well as those at other captive breeding facilities, were paired by using procedures developed by the WGFD. This involved pairing of animals at night with a high degree of human intervention. Staff at the Louisville Zoo tried a different, less intensive approach to male and female pairings that resulted in very successful kit production. In 1996, Center staff decided to conduct a more extensive study comparing the Wyoming and Louisville methods.

In 1996, the entire ferret colony at the Center was kept under strict quarantine procedures during the breeding season. Access to the animals was limited to immediate staff. Additionally, before coming in contact with any ferrets, all employees showered and changed into clothes that remained onsite. Vehicle traffic near the main breeding building was restricted to emergency use in order to minimize possible disturbance to the ferrets.

Black-footed ferret females were divided between the two breeding schemes being investigated (*n* = 36, Wyoming; *n* = 29, Louisville). Only females aged 1–3 years were included in the study, as these age classes form the core of the captive breeding population. All females were housed in the main breeding building and were treated similarly up to the moment of pairing with their chosen male. Each animal was maintained on a strict diet, known as 60/40, which consisted of a mixture of ground rabbit, commercial mink chow, and various additives, formulated by staff of the WGFD prior to 1996. During the breeding season, rendered lard was added to the 60/40 diet of expectant females only. Two months prior to the breeding season, each ferret was weighed and assigned a target weight that was determined by technicians using visual cues of overall body condition. Amount of food provided to the animals was altered based on weight over a 2-month period. As the breeding season progressed, weekly vulvar measurements were performed and recorded. Vaginal cytology and vulva size were used to monitor reproductive readiness in both groups (Williams and others, 1992). In the Louisville method, males were brought to the females' cages and were not given access to the upper nest box at night. Additionally, once a positive sperm check was obtained, the pair was left together for 3 consecutive days and nights. In the Wyoming method, females were brought to the males' cages, confined to the cage surface (1.2 × 1.2 m), which contained a breeding box, and separated from the males during daylight hours.

Peterson (1996) summarized findings of this study for the FWS's 1996 annual progress report. Fecundity, defined as the proportion of bred females that whelped, was higher with the Louisville method (55 percent versus 36 percent). The average litter size per female bred with the Louisville method was 2.65 ± 2.31 (mean ± SE), which was significantly different from the average litter size for the Wyoming breeding method (1.46 ± 1.82; one-way ANOVA, $P = 0.05$). The average number of kits weaned per whelping female with the Louisville method was 3.13 ± 1.93, which was significantly different from results of the Wyoming method (1.54 ± 1.56; one-way ANOVA, $P = 0.02$).

The higher whelping rate and greater number of kits produced with the Louisville method indicated that this management scheme would be beneficial to overall program goals—maintenance of genetic diversity and production of as many kits as possible. Greater kit production with the Louisville method could be a result of several factors, including less stress because of minimal human interactions while males and females were paired and more time for the animals to copulate, as black-footed ferrets are induced ovulators. Pairs were observed copulating multiple times throughout the day, perhaps providing greater stimuli for ovulation to occur. There is also a cost savings associated with the Louisville method, as additional staff are no longer necessary to monitor pairs at night. Daytime ferret keepers balance activities related to ferret breeding with husbandry chores. The Louisville method has now become standard operating procedure at all captive breeding institutions. At the Center, further refinements have occurred during the past several years to make pairings more efficient. Testicular and vulvar measurements have been discontinued in favor of electroejaculation and vaginal cytology to determine male and female reproductive readiness. Video monitoring has also been discontinued. Sperm checks are now performed opportunistically, and staining (Dip Quick; Jorgensen Laboratories, Inc., Loveland, Colo.) is used to determine the success of pairings.

Nutrition

Black-footed ferrets rely predominantly on prairie dogs (*Cynomys* spp.) for food in the wild (Campbell, 1987). Logistically, it would be extremely difficult to feed all ferrets maintained in the captive breeding program a diet of 100 percent prairie dogs, so alternative diets have been investigated. Initially, captive ferrets were fed a mink chow and rabbit-based diet (the aforementioned 60/40 diet) that included a variety of additives thought to be important for maintaining a healthy breeding population based on information from domestic ferret (*Mustela putorius furo*) and mink (*M. vison*) captive breeding programs. As additional captive breeding facilities were incorporated into the program, feeding strategy guidelines and protocols were relaxed. Several nutritionists were concerned that the 60/40 diet had excessive polyunsaturated fatty acids. Oyarzun and others (1994) analyzed and evaluated common diets used throughout the captive breeding program in the mid-1990s and determined that the 60/40 diet used at the Metro Toronto Zoo (now the Toronto Zoo) greatly exceeded dietary recommendations established for mink as well as nutrient levels reported in the natural diet of black-footed ferrets (Dierenfeld and McGuire, 1989). Oyarzun and others (1994) stated that, even though mineral levels were not high enough to cause acute toxicosis, feeding of higher than recommended levels over an extended period of time might have adverse effects (Lyster and others, 2002). Nutritionists at the Toronto Zoo continued to alter the diet composition so that it more closely fit accepted dietary requirements. This research led to formulation of the horse-based Toronto Zoo Small Carnivore Diet produced by Milliken Meat Products, Ltd., Scarborough, Ontario, Canada.

In 2000, a study was conducted at the Center to compare the two diets (60/40 and Toronto Zoo Small Carnivore) used in the captive breeding program. The primary objective of the study was to examine the effect of the diets on reproductive output. As sample sizes were small (four females and four males in each group), we were looking only for obvious and detrimental deviations from results achieved with the standard 60/40 diet. Larger sample sizes would have provided greater statistical power; however, using additional females in the study might also have reduced our ability to maintain genetic diversity and produce kits for reintroduction. Supplemental vitamin K, believed to decrease the frequency of intra-abdominal hemorrhage (blue-belly) in kits, was provided to bred and nursing females at the same dose and time period for both groups. A less labor-intensive strategy to raise kits was used on all litters at the Center. This strategy not only reduced handling time but also decreased the amount of supplemental diet offered to individual kits. Weights of adults were only monitored during preliminary stages of the study to determine adequate serving sizes and guard against large fluctuations in weight. For females, the number of kits born and those surviving to 50 days of age were examined. Fifty days of age was chosen as a cutoff point for the study because all kits are fed identical diets beginning at that age. The response variable for males was number of sperm per milliliter in ejaculate.

A key advantage to the Toronto Zoo Small Carnivore Diet is that it is made under strict quality control (Canadian Food Inspection Agency). The prepackaged diet was found to be very convenient to use, less labor intensive, and more sanitary than the 60/40 diet produced in-house. The majority of ferrets readily accepted the diet and seemed to prefer it at first feeding. Overall, there was no difference between the two diets in the number of kits born per female (3.5) or the number of kits per female surviving to 50 days of age (3.25). Sperm production appeared to be lower in males fed the Toronto Zoo Small Carnivore Diet, but concentrations were above acceptable limits (250×10^6 sperm/mL). Staff at the Center also noticed that kits readily ate the Toronto Zoo Small Carnivore Diet at early stages of development.

Based on these feeding trials in 2000, the Toronto Zoo Small Carnivore Diet was determined to be effective and convenient for use at the Center and replaced the 60/40 diet; however, in 2003 the United States banned import of all meat products from Canada as a result of mad cow disease (bovine spongiform encephalopathy). Accordingly, we investigated alternative diets, including the Dallas Crown Carnivore Diet (Dallas Crown, Inc., Kaufman, Tex.). Earlier feeding trials at the Phoenix Zoo found this diet to be suitable for ferret maintenance and production. The SSP Nutrition Advisory Group also endorsed the diet as an acceptable alternative if the Toronto Zoo Small Carnivore Diet was unavailable. In keeping with our efforts to improve management in the captive breeding program, in 2004 we also evaluated the effect of the Toronto and Dallas Crown diets on sperm production and compared the results to those from black-footed ferrets fed a more natural diet of prairie dogs. There were no significant differences in the response variable among any of the three diets. The Toronto Zoo Small Carnivore Diet is generally preferred by ferret caretakers because of its more even consistency, which makes it easier to feed to ferrets.

Vaccination

Transport of black-footed ferrets across State and international borders may require rabies vaccination, depending on individual State or country regulations. If required, black-footed ferrets over 3 months of age are vaccinated with Imrab® 3 (Merial, Inc., Athens, Ga.). This vaccine is approved for use in domestic ferrets and recommended for yearly revaccination. It is also recommended that ferrets in outdoor pens be vaccinated in areas where rabies is endemic. Rabies vaccination must be by or under the direct supervision of a licensed veterinarian.

Prevention of canine distemper in captive black-footed ferrets has been an important management consideration since the inception of the captive breeding program. Captive ferrets have succumbed to both natural (Williams and others, 1988) and vaccine-induced canine distemper virus (CDV) infections (Carpenter and others, 1976). The search for a safe and effective canine distemper vaccine for use in captive and free-ranging black-footed ferret populations has been a priority for ferret recovery (Wimsatt and others, this volume).

Historically, ferrets in the captive breeding program were vaccinated against CDV with an inactivated virus plus adjuvant. The vaccine was prepared yearly by Dr. M.J.G. Appel of Cornell University. Adjuvant was prepared separately. This vaccine was used until 2002, but no data on duration of immunity and protection against CDV were collected. The recent availability of a commercial, monovalent, canary pox-vectored vaccine for use in domestic ferrets, PureVax® Ferret Distemper Vaccine (Merial, Inc., Athens, Ga.), provided a new possibility for vaccination of captive black-footed ferrets. The vaccine had been tested in the Siberian polecat (*Mustela eversmannii*), a species closely related to the black-footed ferret, with promising results (Wimsatt and others, 2003).

Since management of young black-footed ferrets varies according to their ultimate fate (i.e., release to the wild or captive breeding), we examined several different paradigms of vaccination and the resultant serum neutralization titers. Vaccine used in these studies was a generous donation from Merial. The Wyoming State Veterinary Laboratory in Laramie performed serum neutralization titers.

Three groups of young of the year black-footed ferrets were used. Group 1 consisted of 13 ferrets from multiple litters. These animals were vaccinated intramuscularly with PureVax Ferret Distemper Vaccine. Vaccinations were administered in the right thigh at approximately 60, 74, and 88 days of age. Blood for titers was drawn from the external jugular vein of anesthetized ferrets every 2 weeks, coinciding with vaccinations to minimize handling of young animals. Final blood samples were drawn 2 weeks after the last vaccination. Group 2 included 12 ferrets subjected to vaccination and blood sampling protocols identical to those for group 1, except the PureVax vaccine was given subcutaneously. Group 3 consisted of nine animals subjected to a protocol chosen to approximate the preconditioning of young ferrets for release to the wild. Young preconditioned ferrets are placed in outdoor pens at an early age and often not recaptured for months. Ferrets in this group were vaccinated subcutaneously at 60 days of age and again at 120 days of age. Blood samples were taken at initial vaccination and at 74, 120, and 134 days.

Serum neutralization titers of >1:128 are considered protective (E. Williams, oral commun., 1999). Prior to vaccination, all groups had median titers of <1:8. All ferrets developed protective titers of >1:128 following the second vaccination. Subsequent vaccinations resulted in increased titers. Ten of the ferrets that received intramuscular injections of PureVax were tested 1 year postvaccination, and eight (80 percent) had protective titers.

Results of these studies indicate that black-footed ferrets vaccinated with a minimum of two doses of PureVax Ferret Distemper Vaccine developed protective titers. Three doses of vaccine resulted in increased titers and provided 80 percent of vaccinated ferrets with protective titers up to 1 year later. Based on these results, captive breeding facilities are now encouraged to administer a minimum of two canine distemper vaccinations in young ferrets, beginning at the age of 60 days.

Conclusions

It is apparent that black-footed ferret captive breeding facilities benefit from a flexible management approach. The ability of the program to use adaptive techniques in all areas of ferret management is inextricably linked to the success of reintroduction activities. A stable captive breeding population and an increased number of reintroduction sites have allowed facilities to be more creative in their management decisions. Changes in the program are acceptable only if they do not have a detrimental effect in terms of overall production of animals. Production of kits has been consistent over time, and weaning success continues to improve. Many other changes have been made throughout the history of captive management, including the use of ALPHA-dri™ bedding material (Shepherd Specialty Papers, Watertown, Tenn.), elimination of additional vitamin K supplement, and less labor-intensive dietary management of kits. We will continue to assess our methods on an annual basis and adapt our management in order to provide a stable source of animals to meet the ever-changing needs of the black-footed ferret recovery program.

References Cited

Ballou, J.D., 1984, Strategies for maintaining genetic diversity in captive populations through reproductive technology: Zoo Biology, v. 3, p. 311–323.

Ballou, J.D., and Oakleaf, R., 1989, Demographic and genetic captive-breeding recommendations for black-footed ferrets, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 247–267.

Campbell, T.M., 1987, Food habits of Wyoming black-footed ferrets: American Midland Naturalist, v. 117, p. 208–210.

Carpenter, J.W., Appel, M.J.G., Erickson, R.C., and Novilla, M.N., 1976, Fatal vaccine-induced canine distemper virus infection in black-footed ferrets: Journal of the American Veterinary Medical Association, v. 169, p. 961–964.

Dierenfeld, E.S., and McGuire, J.T., 1989, Seasonal variation in prairie dog carcass composition: New York Zoological Society, 33 p.

Lyster, J., Lockhart, M., Marinari, P., and Garelle, D., eds., 2002, Black-footed ferret husbandry manual: Unpublished report available from the National Black-footed Ferret Conservation Center, 118 p.

Miller, B., Reading, R.P., and Forrest, S., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Oyarzun, S.E., Self, K., Valdes, E.V., Carnio, J.S., Shamir, A.B., Wrobel, M., and Musson, A., 1994, Black-footed ferret SSP 1994 nutrition report for the Metro Toronto Zoo: Toronto, Metro Toronto Zoo, 20 p.

Peterson, D., 1996, A comparison of black-footed ferret (*Mustela nigripes*) productivity under different captive management regimes: Laramie, Wyo., U.S. Fish and Wildlife Service, 26 p.

Russell, W.C., Thorne, E.T., Oakleaf, R., and Ballou, J.D., 1994, The genetic basis of black-footed ferret reintroduction: Conservation Biology, v. 8, p. 263–266.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

Williams, E.S., Thorne, E.T., Appel, M.J.G., and Belitsky, D.W., 1988, Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming: Journal of Wildlife Diseases, v. 24, p. 385–398.

Williams, E.S., Thorne, E.T., Kwiatkowski, D.R., Lutz, K., and Anderson, S.L., 1992, Comparative vaginal cytology of the estrous cycle of black-footed ferrets (*Mustela nigripes*), Siberian polecats (*M. eversmanni*), and domestic ferrets (*M. putorius furo*): Journal of Veterinary Diagnostic Investigation, v. 4, p. 38–44.

Wimsatt, J., Biggins, D., Innes, K., Taylor, B., and Garell, D., 2003, Evaluation of oral and subcutaneous delivery of an experimental canarypox recombinant canine distemper vaccine in the Siberian polecat (*Mustela eversmanni*): Journal of Zoo and Wildlife Medicine, v. 34, p. 25–35.

Wisely, S.M., 2001, Conservation biology of the black-footed ferret (*Mustela nigripes*)—changes in genetic diversity and morphology before, during and after a population bottleneck: Laramie, University of Wyoming, Ph.D. dissertation, 94 p.

Use of Reproductive Technology for Black-footed Ferret Recovery

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Abstract

Assisted reproductive techniques such as artificial insemination (AI), in vitro fertilization, and sperm cryopreservation have been postulated to be "high-tech" strategies for saving endangered species from extinction; however, there has been limited application of assisted breeding in wildlife management. This report illustrates how reproductive technology has been utilized in an integrated conservation program to save the endangered black-footed ferret (*Mustela nigripes*). Considered extinct until a remnant population was discovered in Wyoming in 1981, the last remaining 18 black-footed ferrets were captured to establish a captive breeding program. In 1988, the U.S. Fish and Wildlife Service developed a Black-footed Ferret Recovery Plan, which emphasized species preservation through natural breeding, development of assisted reproductive technology, and establishment of multiple reintroduction sites, among others. A multi-institutional propagation program has been highly successful. Approximately 250 animals currently reside in six breeding facilities, and >500 black-footed ferrets survive in the wild from reintroduced animals. Methods for semen collection, AI, and sperm cryopreservation were developed first in domesticated ferrets (*Mustela putorius furo*) and the closely related Siberian polecat (*Mustela eversmannii*) and now are used routinely in black-footed ferret management to (1) assess sperm status prior to natural breeding; (2) circumvent cases of sexual incompatibility; (3) enhance reproduction in nonbreeding individuals to retain existing genetic diversity; (4) increase founder representation; (5) establish a genome resource bank to preserve valuable germ plasm; and (6) produce additional offspring for reintroduction. To date, 128 black-footed ferret kits have been produced by AI using fresh or frozen semen. The black-footed ferret represents a model for reproductive biotechniques contributing to a multidisciplinary species recovery and reintroduction program.

Keywords: artificial insemination, assisted reproduction, genetic management, genome resource banking, semen

Introduction

The value of reproductive technologies to ex situ and in situ wildlife management in helping conserve genetic and biological diversity has been considered for years. Assisted reproductive technologies such as artificial insemination (AI), in vitro fertilization (IVF), embryo transfer, and gamete/embryo cryopreservation offer many advantages for managing small populations, largely by ensuring that all genetically valuable animals reproduce (Ballou, 1984; Howard, 1993, 1999; Wildt and Roth, 1997; Wildt and others, 1997). The potential of assisted reproduction could be enhanced further by developing genome resource banks (repositories of cryopreserved sperm, eggs, and embryos), thus preserving valuable genetic material for future generations. The combined use of assisted breeding and germ plasm banks also has potential for infusing genetic material from wild-born individuals into genetically stagnant ex situ populations or even for exchanging genetic material between isolated wild populations (Holt and others, 1996; Wildt and others, 1997).

Despite these advantages, assisted reproduction has not been used consistently in practical wildlife management and conservation, largely for one reason. Until recently, no wildlife species had been sufficiently studied that its reproductive biology was so comprehensively understood that assisted breeding could become routine. It commonly is assumed that reproductive knowledge and techniques established for laboratory rodents, domestic farm species, and even humans are readily adaptable to propagating or overcoming infertility in wild animals (Wildt and others, 2001a,b). This is a misperception because all species have naturally evolved, unique, species-specific reproductive mechanisms, most of which have not yet been elucidated. Without such specific information, no assisted breeding technique can ever become routine.

There still is a need to demonstrate how such reproductive strategies can be used pragmatically. In this paper, we demonstrate how management and conservation of an endangered carnivore, the black-footed ferret (*Mustela nigripes*), have benefited from the application of the reproduc-

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tive sciences, including assisted breeding. We assert that the lessons learned from (1) working in partnership with wildlife managers and ex situ breeding institutions, (2) taking a systematic basic and multidisciplinary research approach, and (3) integrating knowledge have helped to recover and reintroduce this endangered species into nature.

Black-footed Ferret Recovery

Between the fall of 1985 and spring of 1987, the Wyoming Game and Fish Department, in cooperation with the U.S. Fish and Wildlife Service, captured the last 18 free-ranging black-footed ferrets from Meeteetse, Wyo., a location known to have sylvatic plague and canine distemper (Forrest and others, 1988; Williams and others, 1988; Thorne and Oakleaf, 1991). In the spring of 1987, captive breeding was successful, and two litters of black-footed ferret kits were born. Given the species' critical status, a recovery plan for ex situ propagation and reintroduction was a high priority. A workshop was held in 1986, facilitated by the Conservation Breeding Specialist Group (CBSG) of the Species Survival Commission of the World Conservation Union (International Union for the Conservation of Nature and Natural Resources). Widespread stakeholder participation was emphasized, and the workshop was attended by representatives from State and Federal wildlife and land management agencies as well as experts in mustelids, small population biology, reproduction, nutrition, veterinary medicine, and genetics. Using workshop information (Seal and others, 1989), the U.S. Fish and Wildlife Service developed an official Black-footed Ferret Recovery Plan in 1988 (U.S. Fish and Wildlife Service, 1988) that emphasized species preservation through research, a multi-institutional ex situ propagation program, and establishment of multiple reintroduction sites. The goal of the ex situ breeding program was to maintain ~240 ferrets (90 males, 150 females) in captivity but in multiple institutions to avoid a catastrophe that might affect any single facility. The aim of the eventual reintroduction program was to establish a total of 1,500 ferrets in at least 10 self-sustaining, free-ranging populations by the year 2010. The wild populations, scattered geographically within the ferret's former range, each were to be composed of at least 30 breeding adults.

Throughout discussions of the ex situ and (eventually) in situ metapopulation structure, the role of sound scientific research, including the potential of reproductive technologies, was always recognized. Managers were especially keen to determine whether such techniques could be useful for evaluating fertility and for developing AI with fresh or cryopreserved spermatozoa, all for the purpose of supporting ex situ breeding and especially avoiding further losses in genetic diversity. One early concept was to establish a black-footed ferret genome resource bank, a frozen repository of spermatozoa from the most genetically valuable males, especially those that failed to reproduce by natural breeding.

Ex Situ Natural Breeding

Intensive management by the Wyoming Game and Fish Department resulted in production of offspring in 1987 and all subsequent years, which allowed dividing the ex situ population into six subcolonies at zoological institutions in North America. The U.S. Fish and Wildlife Service assumed the responsibility of managing the Wyoming breeding facility in 1996 and renamed it the National Black-footed Ferret Conservation Center. Since 1987, the multi-institutional ex situ breeding program has produced >5,100 ferrets (Marinari and Kreeger, this volume) while generating extensive knowledge on ferret biology.

For the past decade, the cooperative effort among the breeding facilities has been guided by the Black-footed Ferret Species Survival Plan® (SSP), a population management strategy of the American Zoo and Aquarium Association designed to maintain a self-sustaining ex situ population while providing animals for reintroduction. Breeding recommendations also are provided in an attempt to equalize genetic representation of the few original wild-born founders. SSP managers determine specific pairs for breeding on the basis of a mean kinship value, a measure of how related an individual is to the remaining population (Ballou and Lacy, 1995; Wisely, this volume). Demographic data, including reproductive lifespan, fecundity, age distribution, and sex ratio, are considered in predicting population stability and growth rate over time. Currently, there are ~250 black-footed ferrets maintained in the SSP program at six locations.

Reintroduction

The ability to produce ferrets in captivity allowed reintroduction to begin in 1991, initially into the Shirley Basin of southeastern Wyoming (Miller and others, 1993; Biggins and others, 1997). A few animals survived over winter, and additional ferrets were released at the same site in subsequent years. In 1995, reintroduction efforts were suspended in Wyoming because of a sylvatic plague outbreak and the loss of vital prairie dog (*Cynomys* spp.) colonies on which the ferrets depend for food and shelter. Subsequent ferret reintroduction sites were established in Conata Basin in South Dakota (Badlands National Park and Buffalo Gap National Grassland in 1994) and Montana (Charles M. Russell National Wildlife Refuge in 1994; Fort Belknap Indian Reservation in 1996). Arizona became the fourth State in the reintroduction program in 1996 with ferret releases in Aubrey Valley. Utah was added as the fifth State in 1999 when ferrets were released in Coyote Basin near the Colorado border. In the fall of 2000, the Cheyenne River tribal lands in South Dakota received ferrets. After extensive planning, a site near Janos, Chihuahua, Mexico, received releases in 2001. Successful reproduction and offspring produced in the wild from released ferrets have been documented at all release sites. Survival of released ferrets has improved because of preconditioning, the exposure of ferrets to large outdoor pens with prairie dog burrow systems and live prey prior to reintroduction. Although success varies, the highest survival has occurred at Conata Basin (South Dakota), with >70 percent of captive-born kits and >90 percent of identified wild-born kits surviving over winter and through spring (T. Livieri, oral commun., 2005). As of fall 2005, the wild population was ~500 black-footed ferrets (T. Livieri, oral commun., 2005).

Development of Reproductive Technologies in Animal Models

Potential benefits of reproductive technologies were recognized from the onset of the recovery program. The recovery plan of 1988 (U.S. Fish and Wildlife Service, 1988), the original and official guide for species rescue, encouraged development of methods for reproductive assessment and assisted breeding. It was realized that AI with fresh or frozen spermatozoa could help retain genetic diversity by ensuring reproduction in every valuable individual that failed to breed naturally. Additionally, a genome resource bank containing cryopreserved spermatozoa could preserve extant genes for the future, as well as assist in the genetic management of this small population.

The National Zoological Park's Conservation & Research Center was invited to take a lead role in studying ferret reproductive biology as well as to participate in the ex situ breeding program. We began our reproductive investigations by using the domestic ferret (*Mustela putorius furo*) and the closely related Siberian polecat (*Mustela eversmannii*) as animal models, first to understand general ferret biology and then to use that knowledge for developing assisted breeding (Wildt and others, 1986). Molecular analyses revealed that the domestic ferret, the Siberian polecat, and the black-footed ferret are taxonomically related (O'Brien and others, 1989). All of these species are seasonal breeders with reproductive activity stimulated by long-day photoperiod (Hillman and Carpenter, 1983; Miller and others, 1988; Mead and others, 1990; Miller and Anderson, 1990; Carvalho and others, 1991). Testis size gradually increases beginning in January or February, peaks from March through June and then gradually declines (Neal and others, 1977). The female's breeding season is monoestrus and restricted to the months of March to June, and is characterized by changes in vaginal cytology and an increase in vulvar size. Finally, these species are classified as induced ovulators, with ovulation occurring ~30 hours after a single copulation or an injection of human chorionic gonadotrophin (hCG) or luteinizing hormone (LH) (Mead and others, 1988).

Extensive studies were conducted on domestic ferrets to develop a reliable approach for collecting, processing, and analyzing fresh or cryopreserved spermatozoa (Curry and others, 1989; Wildt and others, 1989; Howard and others, 1991; Van der Horst and others, 1991). More than 300 electroejaculates from nine males were collected to address the (1) effect of temporal spermatogenesis patterns on sperm viability; (2) comparative effectiveness of vaginal versus uterine insemination via an atraumatic laparoscopic approach; (3) influence of sperm number, dilution medium, and time of hCG administration on pregnancy success, gestation interval, and number of offspring produced; and (4) influence of cryodiluent, freezing method, and thawing temperature on the biological competence of frozen-thawed ferret spermatozoa (Wildt and others, 1989; Howard and others, 1991; Howard, 1999). Such basic studies were crucial to developing reliable assisted breeding techniques. An effective electroejaculation protocol was developed in the domestic ferret to consistently collect high-quality spermatozoa from anesthetized males (table 1). Vaginal insemination was determined to be ineffective for producing offspring; none of 10 females became pregnant after spermatozoa were deposited intravaginally (Wildt and others, 1989). In contrast, transabdominal-intrauterine sperm deposition via laparoscopy resulted in high pregnancy success. Seventeen of 24 ferrets (70.8 percent) inseminated in this fashion became pregnant and delivered live young (Wildt and others, 1989). In addition, embryo transfer was developed in the domestic ferret to nonsurgically transfer preimplantation embryos (Wildt and Goodrowe, 1989; Kidder and others, 1999). Comparative assessments of 12 cryopreservation methods determined that a combination of an egg-yolk/lactose cryodiluent, the pellet freezing method, and a 37°C thawing temperature was effective for freeze-thawing ferret sperm and recovering maximal motility and acrosomal integrity.When this cryomethod was

Table 1. Mean (± SE) ejaculate traits, sperm morphology, and acrosomal integrity in the domestic ferret (*Mustela putorius furo*), Siberian polecat (*M. eversmannii*), and black-footed ferret (*M. nigripes*).

	Domestic ferret (n = 4 males)[a]	**Siberian polecat (n = 8 males)[b]**	**Black-footed ferret (n = 97 males)[b]**
Sperm motility (%)	80.7 ± 1.0[c]	80.6 ± 2.9[c]	51.2 ± 1.8[d]
Sperm progression (0–5; 5 = best)	3.3 ± 0.1	3.0 ± 0.2	2.5 ± 0.1
Normal sperm (%)	67.3 ± 1.3[c]	74.5 ± 2.6[c]	21.0 ± 1.5[d]
Normal intact acrosome (%)	92.4 ± 0.5[c]	96.8 ± 1.0[c]	67.2 ± 2.8[d]

[a] Data based on 52 ejaculates from four males (Howard and others, 1991).

[b] Data based on one ejaculate per male (Howard and others, 1996; J. Howard, unpub. data, 1996).

[c,d] Within rows, values with different superscripts are different ($P < 0.05$).

used, 7 of 10 females (70.0 percent) inseminated in utero with frozen-thawed ferret spermatozoa became pregnant (Howard and others, 1991). Overall, reproductive efficiency was high (70.6 percent) after laparoscopic intrauterine AI with fresh or frozen semen (table 2).

The strategy developed for the domestic ferret was subsequently applied to the Siberian polecat and finally to the black-footed ferret. Although sperm motility traits were similar among the three species, there were significantly fewer structurally normal spermatozoa in the black-footed ferret compared to the domestic ferret and polecat (table 1; Howard and others, 1991, 1996). After cryopreservation and thawing, sperm motility and membrane integrity also were less in the black-footed ferret compared to the other species (Howard and others, 1991, 1996). These differences in sperm viability were assumed to be related to the restricted founder base and reduced genetic variation in the black-footed ferret. Nevertheless, the laparoscopic intrauterine AI technique, developed in the domestic ferret, proved effective in its close relatives. Eight of 10 (80.0 percent) Siberian polecats inseminated with fresh or cryopreserved semen became pregnant (table 2), and this high rate provided the confidence to apply the procedure to the rarer black-footed ferret. Four of six (66.7 percent) black-footed ferrets inseminated with fresh or frozen-thawed semen became pregnant and delivered live young (table 2) (Howard and others, 1996; Howard, 1999).

Table 2. Comparison of laparoscopic intrauterine artificial insemination with fresh or frozen-thawed spermatozoa in closely related ferret species. Data from Wildt and others (1989), Howard and others (1991, 1996), and Howard (1999).

	Domestic ferret (*Mustela putorius furo*)	**Siberian polecat (*Mustela eversmannii*)**	**Black-footed ferret (*Mustela nigripes*)**
Number of females inseminated	34	10	6
Number of pregnant females	24	8	4
Pregnancy rate (%)	70.6	80.0	66.7
Number of kits born	116	42	9
Mean (± SE) number of kits/litter	4.8 ± 0.8	5.2 ± 1.0	2.3 ± 0.6

Assisted Breeding to Enhance Reproduction in Black-footed Ferrets

It soon was realized that the reintroduction goal (1,500 breeding ferrets in 10 free-ranging populations by the year 2010) was not achievable at the current rate of propagation in the ex situ natural breeding program. Early experiences revealed that some animals consistently failed to reproduce. Analysis of breeding records indicated that most females (>90 percent) demonstrated a spring estrus on the basis of vaginal cytology changes (markedly increased numbers of superficial, cornified squamous epithelial cells; fig. 1) (Williams and others, 1992; Brown, 1997); however, there was a high incidence (~40 percent) of pseudopregnancy wherein matings were observed (via video camera) and ovulation was confirmed (by an abrupt decrease in superficial cornified cells), but no pregnancy occurred (Williams and others, 1991). Fecal oestradiol and progestogen metabolite profiles in pregnant versus pseudopregnant females were similar (fig. 1; Brown, 1997), suggesting that endocrine dysfunction was not contributing to the problem.

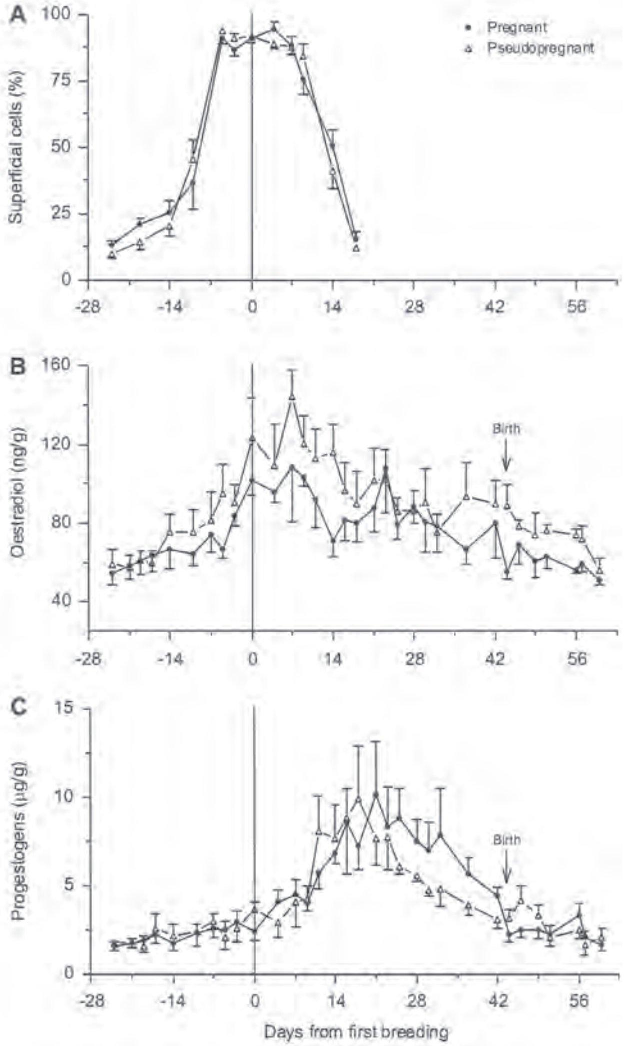

Figure 1. Mean (± SE) percent superficial cells in vaginal lavages (A) and fecal oestradiol (B) and progestogen (C) metabolite concentrations in pregnant (n = 7) and pseudopregnant (n = 9) black-footed ferrets (*Mustela nigripes*). Day 0 is the time of first mating. (From Brown, 1997. Reprinted with permission of the *Journal of Wildlife Management*.)

Interestingly, records analysis indicated that a remarkably high proportion (>50 percent) of prime breeding-age males (1–3 years old) inexplicably failed to sire offspring in captive breeding situations. In 1995, there were 40 such adult males (54.8 percent of the breeding-age male population) that were exposed to prime age, estrual females and yet did not produce young. Simultaneous evaluations also revealed a genetic problem, largely that one of the original wild-born ferret founders was poorly represented in the modern population. This underrepresented lineage had only 43 descendants compared to more than 300 descendants from each of the remaining founder lineages. To help preserve original gene diversity, it was imperative to balance founder representation. This situation was confounded by another challenge in the underrepresented lineage—these males were consistently sexually incompatible with designated mates, largely because of aggression. Together, these issues prompted an examination of the value of reproductive technology and assisted breeding.

At the request of black-footed ferret managers, we agreed to (1) assess reproductive traits and breeding behavior in males with proven versus unproven fertility; (2) establish a genome resource bank containing cryopreserved spermatozoa from the most genetically valuable males; and (3) use AI for improving reproductive efficiency in nonbreeders, all for the ultimate purpose of increasing the number of kits for reintroduction. A survey was conducted in 1996 and 1997 to determine the precise number of prime breeding-age males not siring offspring and the reasons for failed reproduction. As in 1995, a high percentage of 1- to 3-year-old males did not sire young in 1996 (38 of 69 males, 55.1 percent) or 1997 (35 of 60 males, 58.3 percent) (Wolf and others, 2000b). Semen evaluations determined that there were no differences in sperm concentration, motility, or morphology between proven and unproven breeders (Wolf and others, 2000b). A detailed review of breeding data revealed that males failed to reproduce because of improper breeding position, behavioral incompatibility (e.g., aggression), and poor testes development (Wolf and others, 2000b). As much of the problem was behaviorally based, we speculated that assisted reproduction could be beneficial for improving reproductive efficiency.

A systematic strategy was used to establish the genome resource bank. Using the computer software program (SPARKS; International Species Information System, Eagan, Minn.) developed for SSP programs, sperm donors could be selected on the basis of founder representation and mean kinship (Ballou and Lacy, 1995; Johnston and Lacy, 1995; Wisely, this volume). High-priority black-footed ferret males were selected for inclusion in the bank, with semen samples collected and cryopreserved for AI (as part of routine management) or for long-term storage (as a hedge repository of valuable genes).

At the National Zoological Park's Conservation & Research Center, the natural breeding program for black-footed ferrets was modified to include AI. The goals were to (1) produce offspring from behaviorally incompatible animals, especially nonbreeding males, to meet reintroduction demands and (2) increase founder representation in the underrepresented lineage. In achieving these goals, other opportunities arose, including examining the impact of male age on reproductive success. From 1996 through 2003, nonbreeding males of high genetic value were chosen as candidates for assisted reproduction. Overall, 66 females were monitored for natural estrus and were administered hCG or LH (to induce ovulation) 5 to 7 days after maximal vulvar swelling and >90 percent superficial cornified vaginal cells. Twelve to 20 hours later, each female was anesthetized and, under laparoscopic observation, inseminated in utero with fresh or frozen-thawed spermatozoa. Five of six (83.3 percent) females inseminated with semen from founder descendants became pregnant and produced 16 kits (table 3). Males were determined to produce excellent quality semen through 5 years of age, 2 years longer than the normal female reproductive life span (Wolf and others, 2000a). Eight of 11 (72.7 percent) females inseminated with semen from 5-year-old males produced 17 kits (table 3). A total of 28 of 49 (57.1 percent) females gave birth to 95 kits following AI with semen from genetically valuable, nonbreeding males (table 3). Overall, AI resulted in 128 additional black-footed ferret kits, offspring that never would have been born from natural mating.

There were other by-products as well. For example, we observed that a high proportion of 1-year-old males produced aspermic (no sperm) ejaculates during the breeding season (Howard and others, 1998). These males experienced increases in seasonal testicular tumescence (albeit somewhat slower than elders; fig. 2) and copulated with females; however, systematic seminal evaluations revealed that these yearlings produced spermic ejaculates at least 4 weeks later in the breeding season than older counterparts (fig. 2). This asynchrony in sperm

Table 3. Use of laparoscopic artificial insemination to enhance propagation in nonbreeding founder descendants, 5-year-old males, and genetically valuable male black-footed ferrets (*Mustela nigripes*) from 1996 through 2003.

	Founder descendants[a] **(*n* = 3 males)**	**5-year-old males**[b] **(*n* = 5 males)**	**Genetically valuable males**[c] **(*n* = 27 males)**
Number of females inseminated	6	11	49
Number of pregnant females (%)	5 (83.3)	8 (72.7)	28 (57.1)
Number of kits born	16	17	95

[a] Males were descendants of a wild-caught founder whose genetic lineage was underrepresented in the ex situ population.

[b] Reproductive competence was assessed in 5-year-old males.

[c] Despite numerous breeding opportunities, reproductive failure in these genetically valuable males was due primarily to behavioral incompatibility (aggression or shyness) or inappropriate breeding position.

production probably influenced the incidence of pseudopregnancy because aspermic males can induce ovulation following copulation. This was an important observation with significant implications for routine ferret management. Until this finding, males used for breeding were selected on the basis of enlarged testis size. Now, only males with spermic electroejaculates are allowed access to females for natural breeding, and introducing this simple semen assessment technique to the management protocol in 1998 resulted in a striking 20 percent increase in pregnancy success and 59 additional kits available for reintroduction (table 4).

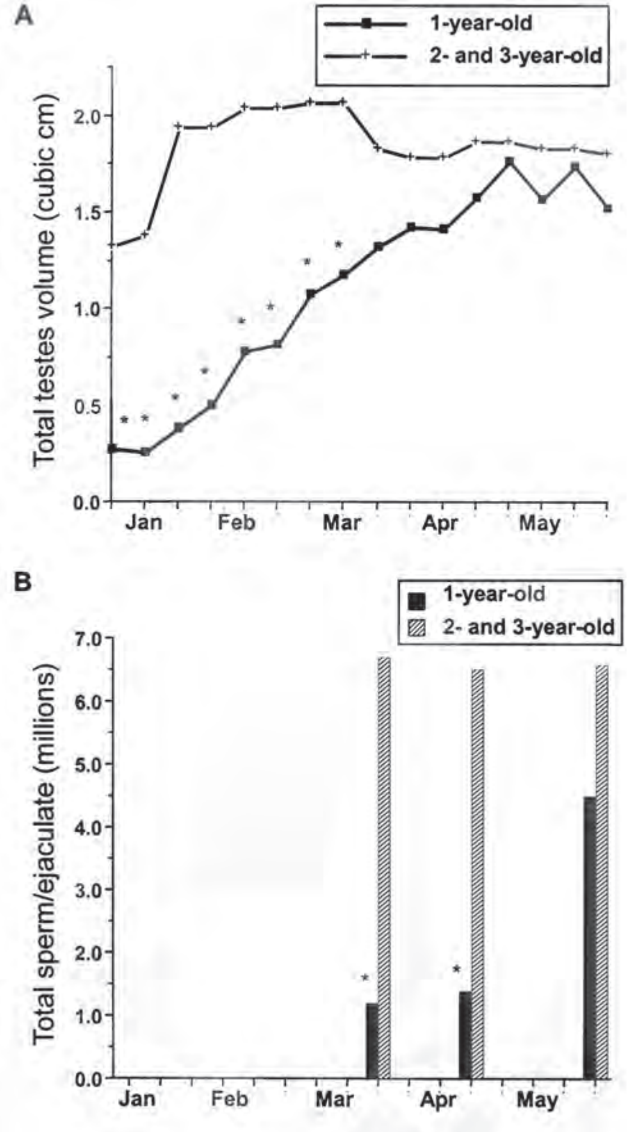

Figure 2. Influence of age on testes development (A) and total sperm/ejaculate (B) in 1-year-old versus 2- and 3-year-old male black-footed ferrets (*Mustela nigripes*). Asterisks indicate differences ($P < 0.05$) between age groups within a month.

Table 4. Propagation in the black-footed ferret (*Mustela nigripes*) using enlarged testes versus spermic ejaculate as the criterion for selecting males for natural breeding.

	Enlarged testes	Spermic ejaculate
Number of females bred	84	86
Number of litters	50	69
Pregnancy success (%)	59.5	80.2
Number of kits born	190	249

Priorities for the Future

The black-footed ferret is a provocative example of how reproductive technologies integrated with both ex situ and in situ management plans can benefit species conservation. The positive results are evidence that reproductive techniques are valuable for (1) generating new knowledge of relevance to natural and assisted breeding and (2) producing living, genetically valuable offspring useful for breeding stock and/or reintroduction. Priorities for this species extend far beyond reproductive biology; adequate survival after reintroduction continues to be essential to the black-footed ferret's future. Urban sprawl, sylvatic plague, and poisoning of prairie dogs appear to be never-ending, severe threats. Today, only 2 percent remains of the ~100 million acres of the original prairie dog ecosystem of the Great Plains (Miller and others, 1996). Monitoring for presence of sylvatic plague as well as canine distemper is essential for long-term protection of both prairie dogs and ferrets. Research into the development and use of a sylvatic plague vaccine is ongoing (Rocke, this volume). Even when a vaccine becomes available, there will be enormous distribution challenges. Also, persistent poisoning campaigns and recreational shooting continue to contribute to the collapse of the prairie dog ecosystem.

Finally, a high priority will continue to be education programs, which play a crucial role in public awareness of black-footed ferret conservation issues. Currently, over 30 zoos and wildlife agencies sponsor educational exhibits, often using "ambassador" black-footed ferrets. Gaining public support, especially from landowners who consider prairie dogs pests, is critical to reintroduction success. Many landowners continue to have serious concerns about endangered species, especially perceived governmental interference and restrictions on land use (Reading and Kellert, 1993; Miller and others, 1996). A key factor facilitating landowner support for ferrets has been the designation of the reintroduced population as experimental and nonessential under the Endangered Species Act (see Lockhart and others, this volume, for additional information). Although resulting in a lower level of protection for released ferrets, this strategy has gained local rancher and farmer cooperation while providing some assurance that reintroduced ferrets and traditional land uses can be compatible.

Conclusion

It is apparent that reproductive sciences can play a vital role in a holistic, integrated conservation program to save an endangered species. The contemporary story of the black-footed ferret illustrates the potential for species recovery and reintroduction based on partnerships and multidisciplinary, sound science. Perhaps most important has been the cooperative feature, collaboration among over 30 organizations, including State and Federal agencies, conservation groups, and zoos, that worked together to return ferrets to their former grassland habitats of the Great Plains. Reproductive technologies, including AI and a genome resource bank, have been integrated successfully into the black-footed ferret recovery program to maintain genetic diversity, enhance reproductive efficiency, and produce additional animals for reintroduction.

Acknowledgments

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References Cited

Ballou, J.D., 1984, Strategies for maintaining genetic diversity in captive populations through reproductive technology: Zoo Biology, v. 3, p. 311–323.

Ballou, J.D., and Lacy, R.C., 1995, Identifying genetically important individuals for management of genetic diversity in pedigreed populations, *in* Ballou, J.D., Gilpin, M., and Foose T.G., eds., Population management for survival and recovery: New York, Columbia University Press, p. 76–111.

Biggins, D.E., Miller, B.J., Clark, T.W., and Reading, R.P., 1997, Conservation management case studies—the black-footed ferret, *in* Meffe, G.K., and Carroll, C.R., eds., Principles of conservation biology: Sunderland, Mass., Sinauer Associates, p. 420–426.

Brown, J.L., 1997, Fecal steroid profiles in black-footed ferrets exposed to natural photoperiod: Journal of Wildlife Management, v. 61, p. 1428–1436.

Carvalho, C.F., Howard, J.G., Collins, L., Wemmer, C., Bush, M., and Wildt, D.E., 1991, Captive breeding of black-footed ferrets (*Mustela nigripes*) and comparative reproductive efficiency in 1-year old versus 2-year old animals: Journal of Zoo and Wildlife Medicine, v. 22, p. 96–106.

Curry, P.T., Ziemer, T., Van der Horst, G., Burgess, W., Straley, M., Atherton, R.W., and Kitchin, R.M., 1989, A comparison of sperm morphology and silver nitrate staining characteristics in the domestic ferret and the black-footed ferret: Gamete Research, v. 22, p. 27–36.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Hillman, C.N., and Carpenter, J.W., 1983, Breeding biology and behavior of captive black-footed ferrets, *Mustela nigripes*: International Zoo Yearbook, v. 23, p. 186–191.

Holt, W.V., Bennett, P.M., Volobouev, V., and Watson, P.F., 1996, Genetic resource banks in wildlife conservation: Journal of Zoology, v. 238, p. 531–544.

Howard, J.G., 1993, Semen collection and analysis in nondomestic carnivores, *in* Fowler, M.E., ed., Zoo and wild animal medicine—current therapy III: Philadelphia, W.B. Saunders Co., p. 390–399.

Howard, J.G., 1999, Assisted reproductive techniques in nondomestic carnivores, *in* Fowler, M.E., and Miller, R.E., eds., Zoo and wild animal medicine IV: Philadelphia, W.B. Saunders Co., p. 449–457.

Howard, J.G., Bush, M., Morton, C., Morton, F., and Wildt, D.E., 1991, Comparative semen cryopreservation in ferrets (*Mustela putorius furo*) and pregnancies after laparoscopic intrauterine insemination with frozen-thawed spermatozoa: Journal of Reproduction and Fertility, v. 92, p. 109–118.

Howard, J.G., Kwiatkowski, D.R., Williams, E.S., Atherton, R.W., Kitchin, R.M., Thorne, E.T., Bush, M., and Wildt, D.E., 1996, Pregnancies in black-footed ferrets and Siberian polecats after laparoscopic artificial insemination with fresh and frozen-thawed semen, *in* Proceedings of the American Society of Andrology, Journal of Andrology, supplement P-51, abstract 115.

Howard, J.G., Wolf, K.N., Marinari, P.E., Kreeger, J.S., Anderson, T.R., Vargas, A., and Wildt, D.E., 1998, Delayed onset of sperm production in 1-year old male black-footed ferrets, *in* Proceedings of the Society for the Study of Reproduction, Biology of Reproduction, supplement 58, abstract 170, p. 124.

Johnston, L.A., and Lacy, R.C., 1995, Genome resource banking for species conservation—selection of sperm donors: Cryobiology, v. 32, p. 68–77.

Kidder, J., Roberts, P.J., Simkin, M.E., Foote, R.H., and Richmond, M.E., 1999, Nonsurgical collection and nonsurgical transfer of preimplantation embryos in the domestic rabbit (*Oryctolagus cuniculus*) and domestic ferret (*Mustela putorius furo*): Journal of Reproduction and Fertility, v. 116, p. 235–242.

Mead, R.A., Joseph, M.M., and Neirinckx, S., 1988, Optimal dose of human chorionic gonadotropin for inducing ovulation in the ferret: Zoo Biology, v. 7, p. 263–267.

Mead, R.A., Neirinckx, S., and Czekala, N.M., 1990, Reproductive cycle of the steppe polecat (*Mustela eversmanni*): Journal of Reproduction and Fertility, v. 88, p. 353–360.

Miller, B., Biggins, D., Hanebury, L., and Vargas, A., 1993, Reintroduction of the black-footed ferret, *in* Mace, G., Olney, P., and Feisner, A., eds, Creative conservation—interactive management of wild and captive animals: London, Chapman and Hall, p. 455–464.

Miller, B., Reading, R.P., and Forrest, S., eds., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Miller, B.J., Anderson, S., DonCarlos, M.W., and Thorne, E.T., 1988, Biology of the endangered black-footed ferret (*Mustela nigripes*) and the role of captive propagation in its conservation—Canadian Journal of Zoology, v. 66, p. 765–773.

Miller, B.J., and Anderson, S.H., 1990, Comparison of black-footed ferret (*Mustela nigripes*) and domestic ferret (*M. putorius furo*) courtship activity: Zoo Biology, v. 9, p. 201–210.

Neal, J.B., Murphy, B.D., Moger, W.H., and Oliphant, L.W., 1977, Reproduction in the male ferret—gonadal activity during the annual cycle—recrudescence and maturation: Biology of Reproduction, v. 17, p. 380–385.

O'Brien, S.J., Martenson, J.S., Eichelberger, M.A., Thorne, E.T., and Wright, F., 1989, Genetic variation and molecular systematics of the black-footed ferret, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds, Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 21–33.

Reading, R.P., and Kellert, S.R., 1993, Attitudes toward a proposed reintroduction of black-footed ferrets (*Mustela nigripes*): Conservation Biology, v. 7, p. 569–580.

Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., 1989, Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, 302 p.

Thorne, E.T., and Oakleaf, B., 1991, Species rescue for captive breeding—black-footed ferret as an example, *in* Gipps, J.H.W., ed., Beyond captive breeding—re-introducing endangered mammals to the wild: Oxford, Clarendon Press, p. 241–261.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

Van der Horst, G., Curry, P.T., Kitchin, R.M., Burgess, W., Thorne, E.T., Kwiatkowski, D., Parker, M., and Atherton, R.W., 1991, Quantitative light and scanning electron microscopy of ferret sperm: Molecular Reproduction and Development, v. 30, p. 232–240.

Wildt, D.E., Brown, J.L., and Howard, J.G., 2001a, Role of reproductive sciences in carnivore conservation, *in* Gittleman, J.L., Funk, S.M., MacDonald, D.W., and Wayne, R.K., eds., Carnivore conservation: Cambridge, Cambridge University Press, p. 359–371.

Wildt, D.E., Bush, M., Morton, C., Morton, F., and Howard, J.G., 1989, Semen characteristics and testosterone profiles in ferrets kept in long-day photoperiod, and the influence of hCG timing and sperm dilution on pregnancy rate after laparoscopic insemination: Journal of Reproduction and Fertility, v. 86, p. 349–358.

Wildt, D.E., Ellis, S., and Howard, J.G., 2001b, Linkage of reproductive sciences—from 'quick fix' to 'integrated' conservation, *in* Concannon, P.W., England, G.C.W., Farstad, W., Linde-Forsberg, C., Verstegen, J.P., and Doberska, C., eds., Advances in reproduction in dogs, cats and exotic carnivores: Colchester, Journal of Reproduction and Fertility, Ltd., p. 295–307.

Wildt, D.E., and Goodrowe, K.L, 1989, The potential for embryo technology in the black-footed ferret, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 160–176.

Wildt, D.E., Rall, W.F., Critser, J.K., Monfort, S.L., and Seal, U.S., 1997, Genome resource banks—living collections for biodiversity conservation: BioScience, v. 47, p. 689–698.

Wildt, D.E., and Roth, T.L., 1997, Assisted reproduction in managing and conserving threatened felids: International Zoo Yearbook, v. 35, p. 164–172.

Wildt, D.E., Schiewe, M.C., Schmidt, P.M., Goodrowe, K.L., Howard, J.G., Phillips, L.G., O'Brien, S.J., and Bush, M., 1986, Developing animal model systems for embryo technologies in rare and endangered wildlife: Theriogenology, v. 25, p. 33–51.

Williams, E.S., Thorne, E.T., Appel, M.J.G., and Belitsky, D.W., 1988, Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming: Journal of Wildlife Diseases, v. 24, p. 385–398.

Williams, E.S., Thorne, E.T., Kwiatkowski, D.R., Anderson, S.T., and Lutz, K., 1991, Reproductive biology and management of captive black-footed ferrets (*Mustela nigripes*): Zoo Biology, v. 10, p. 383–398.

Williams, E.S., Thorne, E.T., Kwiatkowski, D.R., Lutz, K., and Anderson, S.T., 1992, Comparative vaginal cytology of the estrous cycle of black-footed ferrets (*Mustela nigripes*), Siberian polecats (*M. eversmanni*), and domestic ferrets (*M. putorius furo*): Journal of Veterinary Diagnostic Investigations, v. 4, p. 38–44.

Wolf, K.N., Wildt, D.E., Vargas, A., Marinari, P.E., Kreeger, J.S., Ottinger, M.A., and Howard, J.G., 2000a, Age-dependent changes in sperm production, semen quality and testicular volume in black-footed ferrets (*Mustela nigripes*): Biology of Reproduction, v. 63, p. 179–187.

Wolf, K.N., Wildt, D.E., Vargas, A., Marinari, P.E., Ottinger, M.A., and Howard, J.G., 2000b, Reproductive inefficiency in male black-footed ferrets (*Mustela nigripes*): Zoo Biology, v. 19, p. 528.

The Genetic Legacy of the Black-footed Ferret: Past, Present, and Future

By Samantha M. Wisely[1]

Abstract

The black-footed ferret (*Mustela nigripes*) evolved in Beringia sometime in the early to middle Pleistocene. By 35,000 years before present the species was distinct from its sister taxon, the Siberian polecat (*Mustela eversmannii*). Genetic analysis revealed that historical populations had restricted gene flow prior to human disturbance, which had consequences for the conservation of genetic diversity in the species. Most genetic diversity in the species was lost when Great Plains populations were extirpated, leaving the last surviving population genetically distinct and depauperate. Further genetic losses occurred when almost half of the animals captured from the last population failed to breed in captivity. Once established in captivity, however, maintenance of remaining genetic diversity was within the goals of genetic management mandated by the recovery plan. Reintroduced populations of black-footed ferrets maintained genetic diversity, but were slightly differentiated from one another because of differences in population founders. Wild-born animals were less inbred than captive-released animals, suggesting that inbreeding avoidance mechanisms may operate in the wild. Although much diversity has been lost, inbreeding depression has not been confirmed. Future management efforts should maintain vigilance to conserve remaining genetic diversity both in captivity and in reintroduced populations.

Keywords: captive breeding, genetic diversity, genetic drift, Pleistocene refugia, population bottleneck, reintroduction

Introduction

Eighteen years have passed since the first genetic study of the black-footed ferret (*Mustela nigripes*) was completed (Kilpatrick and others, 1986). Although techniques have advanced and our understanding of genetic processes has expanded, the story revealed by this species' genes remains unwaveringly clear: the genetic uniformity measured in this species is unprecedented and rivaled by perhaps only one other carnivore, the cheetah (*Acinonyx jubatus*; O'Brien and others, 1983). Unlike the cheetah, however, whose Holocene population bottleneck remains shrouded in mystery, the black-footed ferret's demise was witnessed and documented by museum collectors, commercial trappers, animal control agents, and biologists (Anderson and others, 1986), providing a clear understanding of the demography of the bottleneck. Although the dramatic nature of the bottleneck was unfortunate for conservation of the species, it provides conservation-based science with the opportunity to study the genetic consequences of rapid and dramatic population loss outside of the laboratory setting.

Population bottlenecks occur when population size is rapidly reduced; the severity of a bottleneck depends on the minimum population size attained and the duration of time it remained small (Frankham and others, 2002). Although the immediate consequence of small population size is increased risk of extinction as a result of demographic stochasticity, long-term consequences result from reduced genetic diversity and increased inbreeding (Frankel and Soulé, 1981). By increasing the expression of deleterious alleles, inbreeding reduces individual fitness, further increasing the likelihood of extinction. Inbreeding depression caused by a population bottleneck has been documented in a variety of species, including the Florida panther (*Puma concolor coryi*; Roelke and others, 1993), fritillary butterflies (*Melitaea cinxia*; Saccheri and others, 1998), and koalas (*Phascolarctos cinereus*; Seymour and others, 2001). Reduced genetic diversity also has the insidious and difficult to measure effect of reducing a species' ability to adapt to a changing environment. Examples in the literature are few but include endemic rainforest fruitflies (*Drosophila* spp.; Hoffman and others, 2003).

The black-footed ferret experienced serious population decline beginning in the mid- to late 1800s as people migrated west and converted grasslands to agriculture. By 1981 only one population remained, and the species reached its nadir in 1987 when the last of 18 individuals were taken into captivity from Meeteetse, Wyo. (Clark, 1994). This was the first time the U.S. Fish and Wildlife Service (FWS) had managed an endangered species by removing all living individuals from the wild. Ironically, FWS made that decision twice in 1987, when the last remaining California condors (*Gymnogyps californianus*; Seal, 1989; Snyder and Snyder, 2000) were also removed from the wild and placed in a captive breeding program. Unfortunately, animal husbandry practices were not fully

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established in the initial years of captive breeding, and only seven founding ferrets are represented in the current captive population (Garell and others, 1998). Nonetheless, more than 4,000 individuals have been produced, and today approximately 240 animals exist in captivity and 500 in the wild. With a founder genome equivalent (the number of unique genomes represented in the current population) of 4.1 (Russell and others, 1994), the species currently contains a fraction of the genetic diversity once present.

Several demographic events transpired to reduce the population size of this species. Habitat conversion, poisoning campaigns aimed at prairie dogs (*Cynomys* spp.), and exotic diseases decreased the population by 99 percent over approximately 100 years. In the last historical population, simultaneous epizootics of canine distemper virus and sylvatic plague (caused by the bacterium *Yersinia pestis*) caused dramatic population decline in less than a year. In order to understand the consequences of these demographic events, one must first understand the context in which they occurred. How much genetic diversity did the species have prior to anthropogenic disturbance? How much genetic diversity did black-footed ferrets have prior to the bottleneck of the Meeteetse population? How did population structure affect the rate of loss of genetic diversity? Once ferrets were taken into a captive breeding program, how well was the remaining genetic diversity conserved? Finally, as reintroduced populations continue to be established, it is crucial to understand how the process of reintroduction affects genetic diversity and structure. In the following chapter, I synthesize what is known about the genetic legacy of this species as it passed through the processes of population bottleneck, captive management, and reintroduction.

Pleistocene Colonization of North America

The black-footed ferret is a relatively recent immigrant to North America via the Bering land bridge (Youngman, 1994). The earliest fossil record of a black-footed ferret in North America is from Cathedral Cave in eastern central Nevada (Owen and others, 2000). This specimen dates approximately 800,000 years before present based on paleomagnetic data and biochronology of arvicoline rodents collected at the site (Owen and others, 2000). In support of a middle Pleistocene invasion, molecular clock estimates based on 41 isozymes suggest that the black-footed ferret split from its sister species the Siberian polecat (Mustela eversmannii) between 0.5 and 2 million years ago (O'Brien and others, 1989). Thus it appears that the ancestral black-footed ferret crossed the land bridge approximately 1 to 2 million years ago. The species gained access to the grasslands and shrublands of North America via an interglacial, ice-free corridor (Anderson, 1989; Youngman, 1994) and was established at least as far south as Nevada by 800,000 years ago. Once established, the species spread rapidly throughout the Great Plains. By 35,000 years before present the black-footed ferret was morphologically distinguishable from the Siberian polecat. In fact, the two species appear to have existed sympatrically; fossils of both species found in eastern Beringia as recently as 35,000 years ago suggest a period of secondary contact after differentiation (Youngman, 1994).

Molecular data suggest that black-footed ferret populations had restricted gene flow and high population differentiation that was influenced by both natural history and the ebb and flow of Pleistocene glaciers (Wisely and others, 2002). Genetic variation becomes partitioned among subpopulations when isolating mechanisms, such as Pleistocene glaciers and unsuitable habitat, prevent gene flow and increase genetic drift (Frankham and others, 2002). Using microsatellite markers, Wisely and others (2002) reported an average F_{ST} of 0.53. F_{ST} is a pairwise measure of genetic variation that is partitioned among populations. This parameter measures genetic structure and gene flow between subpopulations and ranges in value from 0 (no allelic differentiation or structure) to 1 (maximum allelic divergence). The value found for black-footed ferrets is one of the highest reported for a mammalian carnivore and likely reflects aspects of their unusual ecology. Their diminutive body size, coupled with their semifossorial lifestyle, likely limited their dispersal capabilities (when compared to other carnivorans) and therefore induced genetic drift within populations and created genetic differentiation among populations (Wisely and others, 2002). Subpopulation isolation was likely exasperated by habitat barriers that formed during glacial maxima.

Historical Genetic Diversity and Structure

The historical population structure of the black-footed ferret in North America greatly influenced the amount of genetic diversity that was lost. The magnitude of loss of genetic diversity was exasperated by the especially isolated nature of the last population. Located on the periphery of the historical distribution near the town of Meeteetse, Wyo. (Hillman and Clark, 1980), this population was likely a refugium during the last glacial maximum and remained isolated from other populations throughout the Holocene (Wisely and others, 2002). Measures of genetic distance used to estimate genetic differences among black-footed ferrets from three historical populations confirm that the Meeteetse population was the most highly differentiated and therefore isolated of the three populations (Wisely and others, 2002). Thus, when ferret populations from the Great Plains were extirpated, the majority of genetic diversity found in the species was lost (table 1, fig. 1). Indeed, the Meeteetse population was different enough from other ferret populations that the addition of even four individuals from Mellette County, S. Dak. (the second to last population of black-footed ferrets), would have increased allelic diversity in extant ferrets by 50 percent (Wisely and others, 2002).

Table 1. Observed (H_o) and expected (H_e) heterozygosities for 14 microsatellite loci in black-footed ferrets (*Mustela nigripes*) from Wyoming, South Dakota, and Kansas combined (representing the species prior to disturbance; $n = 20$) and from Wyoming only ($n = 12$), and HWE *P*, the probability associated with an exact test of Hardy-Weinberg equilibrium. Seven of 14 loci were monomorphic in the Wyoming population. HWE was tested only in polymorphic loci from Wyoming. (From Wisely and others, 2002. Reprinted with permission of Oxford University Press, Oxford, U.K.)

Microsatellite loci names	Wyoming, South Dakota, Kansas		Wyoming only		
	H_o	H_e	H_o	H_e	HWE *P*
Mvis002	0.65	0.48	0.50	0.39	0.53
Mvis9700	0.33	0.36	0.33	0.39	1
Mvis072	0.47	0.65	0.67	0.58	0.77
Mer095	0.20	0.27	0.17	0.16	1
Mer049	0.35	0.69	0.50	0.51	1
Mvi57	0.10	0.54	0.17	0.16	1
Mvis022	0.11	0.63	0.08	0.23	0.13
Gg4	0.05	0.14	-	-	-
Mvis075	0.17	0.53	-	-	-
Mvi87	0.00	0.43	-	-	-
G1A	0.10	0.19	-	-	-
Mvi232	0.20	0.19	-	-	-
Mer022	0.11	0.45	-	-	-
Mer009	0.06	0.06	-	-	-

Diversity and Structure in Captivity

Although Meeteetse animals were first captured in 1985, successful breeding was not achieved until 1987 (Clark, 1994). Of the 18 animals that survived in captivity, only 8–11 founders (unknown paternity of some wild-caught litters created some uncertainty as to the exact number) were initially represented in the pedigree; 20 years later, only 7 founders are represented in the extant population (Garell and others, 1998). The consequences of this bottleneck were measurable. Had 5 more of the original 18 ferrets bred successfully, genetic diversity of the extant population would have increased by 30 percent (fig. 1; Wisely and others, 2002). Once animal husbandry was understood and disease concerns were alleviated, the population quickly expanded, and the remaining genetic diversity was conserved (Wisely and others, 2003).

The dramatic loss of approximately 90 percent of the species' genetic diversity necessitated conservation of that which remained. Because all captive populations are susceptible to problems associated with small population size, including inbreeding, inbreeding depression, and genetic drift (de Boer, 1994), management of the remaining genetic variation was a high priority (Ballou and Oakleaf, 1989). Various approaches have been used to maximize retention of genetic variability; for the black-footed ferret, the mean kinship strategy augmented with line breeding of underrepresented founders was recommended (Ballou and Oakleaf, 1989). Briefly, mean kinship strategy finds suitable breeding pairs that maximize the representation of the most underrepresented founders of the captive population. Over time, this strategy is predicted to maximally conserve genetic diversity. Empirically, it appears that this strategy has succeeded in adequately preserving genetic diversity. Founders' genes were more evenly represented in the captive population in 1999 than in the first generation of captive black-footed ferrets (fig. 2; Wisely and others, 2003), and even representation of founders maximally conserves genetic diversity in a pedigreed population. Likewise, a pedigree-based estimate of loss of heterozygosity was 12 percent, which meets the goal established by the American Zoo and Aquarium Association's Species Survival Plan® of retaining 80 percent of the genetic diversity of the founding population for 25 years (Garell and others, 1998). Molecular-based estimates revealed no loss of allelic diversity; all alleles present in the founders were present in the extant population (Wisely and others, 2003).

Diversity and Structure of Reintroduced Populations

Once captive-born animals were released into the wild, further challenges faced the recovery program. A successful captive breeding reintroduction program involves substantive

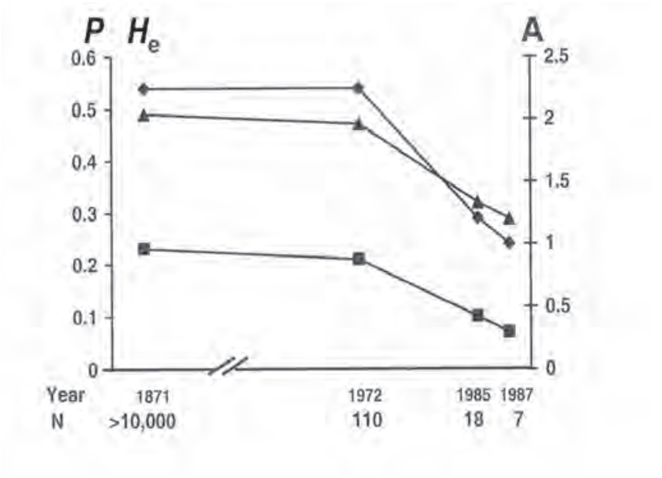

Figure 1. A timeline of genetic diversity in the black-footed ferret (*Mustela nigripes*). A, the average number of alleles per locus (triangle); H_e, expected heterozygosity (diamond); and P, the proportion of polymorphic loci (square) were at their highest values in 1871. In 1972 only two populations remained, in Mellette County, S. Dak., and Meeteetse, Wyo. Note that although many populations throughout the Great Plains were extirpated, genetic diversity did not appreciably decrease. With the loss of the Mellette County population, substantial amounts of genetic diversity were lost. Only the Meeteetse population remained in 1982. Further loss of genetic diversity occurred because of a bottleneck in the last population from 1982 to 1987. (From Wisely and others, 2002. Reprinted with permission of Oxford University Press, Oxford, U.K.)

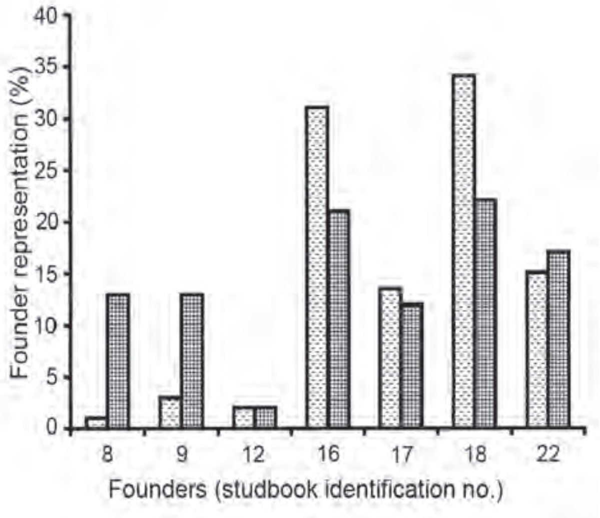

Figure 2. Founder representation in the first generation of captive breeding (i.e., all the direct descendants) (dotted bars) and in 1999, after 14 years of captive breeding (cross-hatched bars) of black-footed ferrets (*Mustela nigripes*). Only founders with genes represented in the extant population are considered. (From Wisely and others, 2003. Reprinted with permission of Wiley-Liss, Hoboken, N.J.)

but reconcilable tradeoffs. Demographic and genetic attributes affect the success of reintroduced populations (Jiménez and others, 1994; FitzSimmons and others, 1997), yet selection of animals for release removes them and their potentially unique genes from the captive breeding pool. This sets up a potential conflict between the goals of captive breeding and reintroduction (Earnhardt, 1999). Because of the tenuous nature of the early captive breeding program and the recognition that captive breeding would need to be maintained for many years, inbred animals and animals with a mean kinship >0.125 were designated for release (Ballou and Oakleaf, 1989). This strategy would maximize retention of genetic diversity in the captive population.

Inbreeding in 1991, estimated from pedigree analysis, was higher in released captive-bred animals ($F = 0.092$) than in animals retained in the captive population ($F = 0.052$; Russell and others, 1994), as would be expected by the designation criteria for animals retained versus released from the captive population. By 1999, overall inbreeding was higher (as would be expected in a small, closed population), but the difference between captive breeders and captive releases was negligible ($F = 0.12$ and 0.11, respectively; Wisely and others, 2003). The gap between breeders and releases was closed because founder genes were more evenly represented in the 1999 than in the 1991 captive population (fig. 2), resulting in a panmictic population. Equal founder representation reduced the variance in mean kinship of individuals, which in turn decreased the difference in genetic composition between breeders and releases (Wisely and others, 2003).

As of 1999, no difference in genetic diversity had been detected between captive-reared releases and their wild descendants from Charles M. Russell National Wildlife Refuge, Mont., and Conata Basin, S. Dak. (table 2; Wisely and others, 2003). This finding suggests that initial releases and subsequent augmentation were sufficient to halt drift-induced losses in diversity. Small but statistically significant population differentiation ($F_{ST} = 0.09$, 95 percent CI = 0.04–0.13) between wild descendants of two reintroduced populations suggested that even with augmentation of captive animals to the reintroduced population, these two populations had measurable genetic differences attributable to random differences in the founders of each reintroduction site (Wisely and others, 2003). Whether this statistically significant difference is also biologically significant is difficult to say (Hedrick, 1999). It is likely, however, that, as populations grow and augmentation ceases, continuing genetic drift will decrease genetic diversity within populations and increase genetic distance among populations.

Because wild-born animals were descended from animals with higher than average mean kinship and inbreeding (as calculated from the pedigree and estimated from microsatellites), it was predicted that the offspring would be inbred. In fact, this was not the case (table 2; Wisely and others, 2003). This result was surprising inasmuch as free ranging populations were smaller than the captive population, released animals were the descendants of overrepresented individuals,

Table 2. Measures of genetic diversity, H_o, the observed heterozygosity, and H_e, the expected heterozygosity, for five groups of black-footed ferrets (*Mustela nigripes*), and HWE *P*, the probability of heterozygote deficiencies (an indicator of inbreeding) within groups. H_e and H_o values were averaged over the seven microsatellite loci that were polymorphic in the historical Wyoming population. Each of the seven loci had two alleles per locus in each group of ferrets. Both captive breeders and captive releases showed evidence of inbreeding as predicted by pedigree-based methods. (From Wisely and others, 2003. Reprinted with permission of Wiley-Liss, Hoboken, N.J.)

Group	*n*	H_o	$H_e \pm 2$ SE	HWE *P*
Founders	7	0.40	0.33 ± 0.14	0.76
Captive breeders	29	0.32	0.41 ± 0.12	0.03
Captive releases	36	0.31	0.38 ± 0.14	0.01
Wild, Montana	81	0.33	0.33 ± 0.14	0.47
Wild, South Dakota	41	0.43	0.38 ± 0.12	0.87

and litter mates often were released together. A possible explanation for the lack of inbreeding in the wild populations is a behavioral response of inbreeding avoidance. Several researchers have proposed that closely related individuals avoid mating in such taxa as black-tailed prairie dogs (*Cynomys ludovicianus*; Hoogland, 1982), olive baboons (*Papio anubis*; Packer, 1979), and the marsupial genus *Antechinus* (Cockburn and others, 1985). Given that the reintroduced founding populations were small and that black-footed ferrets avoided close kin matings, survival and reproduction of founding populations may have been less than optimal as reintroduced individuals avoided breeding with one another and dispersed to find unrelated mates (Wisely and others, 2003).

The Future

The consequence of dramatic loss of genetic diversity in a species is unclear. Some taxa, such as felids, are highly susceptible to inbreeding depression, while other taxa appear unaffected (Ralls and Ballou, 1983; Lacy, 1997). Small, inbreeding populations have a higher rate of expression of deleterious alleles, which can lead to extinction when the forces of genetic drift are greater than natural selection. When selection exceeds drift, however, small, inbreeding populations can purge deleterious alleles, ultimately making them less susceptible to inbreeding depression. To date, no physiological abnormalities have been linked to inbreeding depression in black-footed ferrets, although abnormalities exist (Howard and others, this volume). Indeed, fecundity of females (measured as kits surviving per litter) was virtually the same (3.1–3.3 kits per female) for animals observed in the historical populations of Mellette County, S. Dak. (Hillman and Carpenter, 1980), and Meeteetse, Wyo. (Forrest and others, 1988), and the reintroduced population in Conata Basin, S. Dak. (U.S. Department of Agriculture, 2000).

Without question the two biggest hurdles to recovery of this species are lack of suitable habitat for reintroduction and sylvatic plague (Conservation Breeding Specialist Group, 2004). Where ample, plague-free habitat exists, populations appear to flourish despite reduced genetic diversity. The dramatic loss of genetic diversity in this species should not discourage biologists from planning for recovery. With careful management of remaining genetic resources, this species will likely persist. Continued, vigilant conservation of genetic diversity in the captive population will be critical to the long-term success of this recovery effort. Likewise, genetic management of the reintroduced populations will be critical once populations become self-sustaining. Currently, only two populations are self-sustaining: those of Shirley Basin, Wyo., and Conata Basin, S. Dak. All other reintroduction sites rely on yearly augmentation to maintain their populations. Translocations for genetic augmentation may be necessary if reintroduced populations lose genetic diversity because of drift.

The dramatic loss of genetic diversity in this endangered species should serve as a reminder to conservation practitioners that proactive management of population structure (conserving as many individuals from as many geographic locations as possible) can have a profound effect on the conservation of genetic resources for a species. Furthermore, rapid breeding of as many founders as possible within the first few generations of captive breeding will maximize the retention of the remaining genetic diversity and increase the likelihood of persistence into the future.

Acknowledgments

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References Cited

Anderson, E., 1989, The phylogeny of mustelids and the systematics of ferrets, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 10–20.

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Ballou, J.D., and Oakleaf, R., 1989, Demographic and genetic captive-breeding recommendations for black-footed ferrets, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 247–267.

Clark, T.W., 1994, Restoration of the endangered black-footed ferret—a 20-year overview, *in* Bowles, M.L., and Whelan, C.J., eds., Restoration of endangered species—conceptual issues, planning, and implementation: New York, Cambridge University Press, p. 272–297.

Cockburn, A., Scott, M.P., and Scott, D.J., 1985, Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae): Animal Behaviour, v. 33, p. 908–915.

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

de Boer, L.E.M., 1994, Development of coordinated genetic and demographic breeding programmes, *in* Olney, P.J.S., Mace, G.M., and Feistner, A.T.C., eds., Creative conservation: interactive management of wild and captive animals: New York, Chapman and Hall, p. 304–311.

Earnhardt, J.M., 1999, Reintroduction programmes—genetic trade-offs for populations: Animal Conservation, v. 2, p. 279–286.

FitzSimmons, N.N., Buskirk, S.W., and Smith, M.H., 1997, Genetic changes in reintroduced Rocky Mountain bighorn sheep populations: Journal of Wildlife Management, v. 61, p. 863–872.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–173.

Frankel, O.H., and Soulé, M.E., 1981, Conservation and evolution: New York, Cambridge University Press, 327 p.

Frankham, R., Ballou, J.D., and Briscoe, D.A., 2002, Introduction to conservation genetics: New York, Cambridge University Press, 617 p.

Garell, D., Vargas, A., and Marinari, P., 1998, Black-footed ferret species survival plan—annual report 1997: Bethesda, Md., American Zoo and Aquarium Association, 3 p.

Hedrick, P.W., 1999, Perspective—highly variable loci and their interpretation in evolution and conservation: Evolution, v. 53, p. 313–318.

Hillman, C.N., and Carpenter, J.W., 1980, Masked mustelid: Nature Conservancy News, March–April, p. 20–23.

Hillman, C.N., and Clark, T.W., 1980, Black-footed ferret (*Mustela nigripes*): Mammalian Species, v. 126, p. 1–3.

Hoffman, A.A., Hallas, R.J., Dean, J.A., and Schiffer, M., 2003, Low potential for climatic stress adaptation in a rainforest *Drosophila* species: Science, v. 301, p. 100–102.

Hoogland, J.L., 1982, Prairie dogs avoid extreme inbreeding: Science, v. 215, p. 1639–1641.

Jiménez, J.A., Hughes, K.A., Alaks, G., Graham, L., and Lacy, R.C., 1994, An experimental study of inbreeding depression in a natural habitat: Science, v. 266, p. 271–273.

Kilpatrick, C.W., Forrest, S.C., and Clark, T.W., 1986, Estimating genetic variation in the black-footed ferret—a first attempt: Great Basin Naturalist Memoirs No. 8, p. 145–149.

Lacy, R.C., 1997, Importance of genetic variation to the viability of mammalian populations: Journal of Mammalogy, v. 78, p. 320–335.

O'Brien, S.J., Martenson, J.S., Eichelberger, M.A., Thorne, E.T., and Wright, F., 1989, Genetic variation and molecular systematics of the black-footed ferret, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 21–33.

O'Brien, S.J., Wildt, D.E., Goldman, D., Merril, C.R., and Bush, M., 1983, The cheetah is depauperate in biochemical genetic variation: Science, v. 227, p. 459–462.

Owen, P.R., Bell, C.J., and Mead, E.M., 2000, Fossils, diet, and conservation of black-footed ferrets (*Mustela nigripes*): Journal of Mammalogy, v. 81, p. 422–433.

Packer, C., 1979, Inter-troop transfer and inbreeding avoidance in *Papio anubis*: Animal Behaviour, v. 27, p. 1-36.

Ralls, K., and Ballou, J., 1983, Extinction—lessons from zoos, *in* Schonewald-Cox, C.M., Chambers, S.M., MacBryde, B., and Thomas, L., eds., Genetics and conservation—a reference for managing wild animal and plant populations: Menlo Park, Calif., Benjamin/Cummings, p. 164–184.

Roelke, M.E., Martenson, J.S., and O'Brien, S.J., 1993, The consequences of demographic reduction and genetic depletion in the endangered Florida panther: Current Biology, v. 3, p. 340–350.

Russell, W.C., Thorne, E.T., Oakleaf, R., and Ballou, J.D., 1994, The genetic basis of black-footed ferret reintroduction: Conservation Biology, v. 8, p. 263–266.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W., and Hanski, I., 1998, Inbreeding and extinction in a butterfly metapopulation: Nature, v. 392, p. 491–494.

Seal, U.S., 1989, Introduction, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. xi–xvii.

Seymour, A.M., Montgomery, M.E., Costello, B.H., Ihle, S., Johnsson, G., St. John, B., Taggart, D., and Houlden, B.A., 2001, High effective inbreeding coefficients correlate with morphological abnormalities in populations of South Australian koalas (*Phascolarctos cinereus*): Animal Conservation, v. 4, p. 211–219.

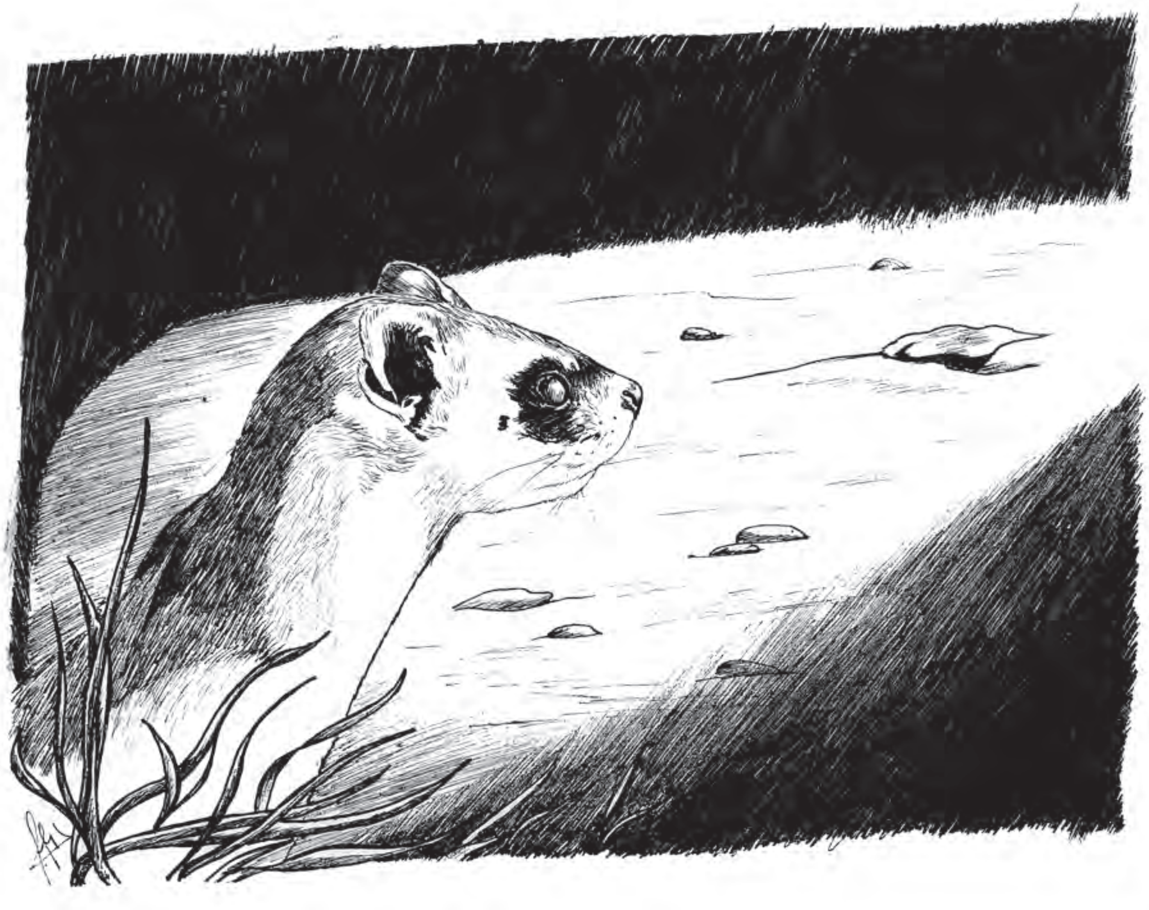
Snyder, N., and Snyder, H., 2000, The California condor—a saga of natural history and conservation: New York, Academic Press, 410 p.

U.S. Department of Agriculture, 2000, Summary of the black-footed ferret program—Conata Basin, Buffalo Gap National Grasslands, South Dakota: Wall, S. Dak., U.S. Department of Agriculture, Forest Service, 4 p.

Wisely, S.M., Fleming, M.A., McDonald, D.B., Buskirk, S.W., and Ostrander, E.A., 2002, Genetic diversity and fitness in black-footed ferrets before and during a bottleneck: Journal of Heredity, v. 93, p. 231–237.

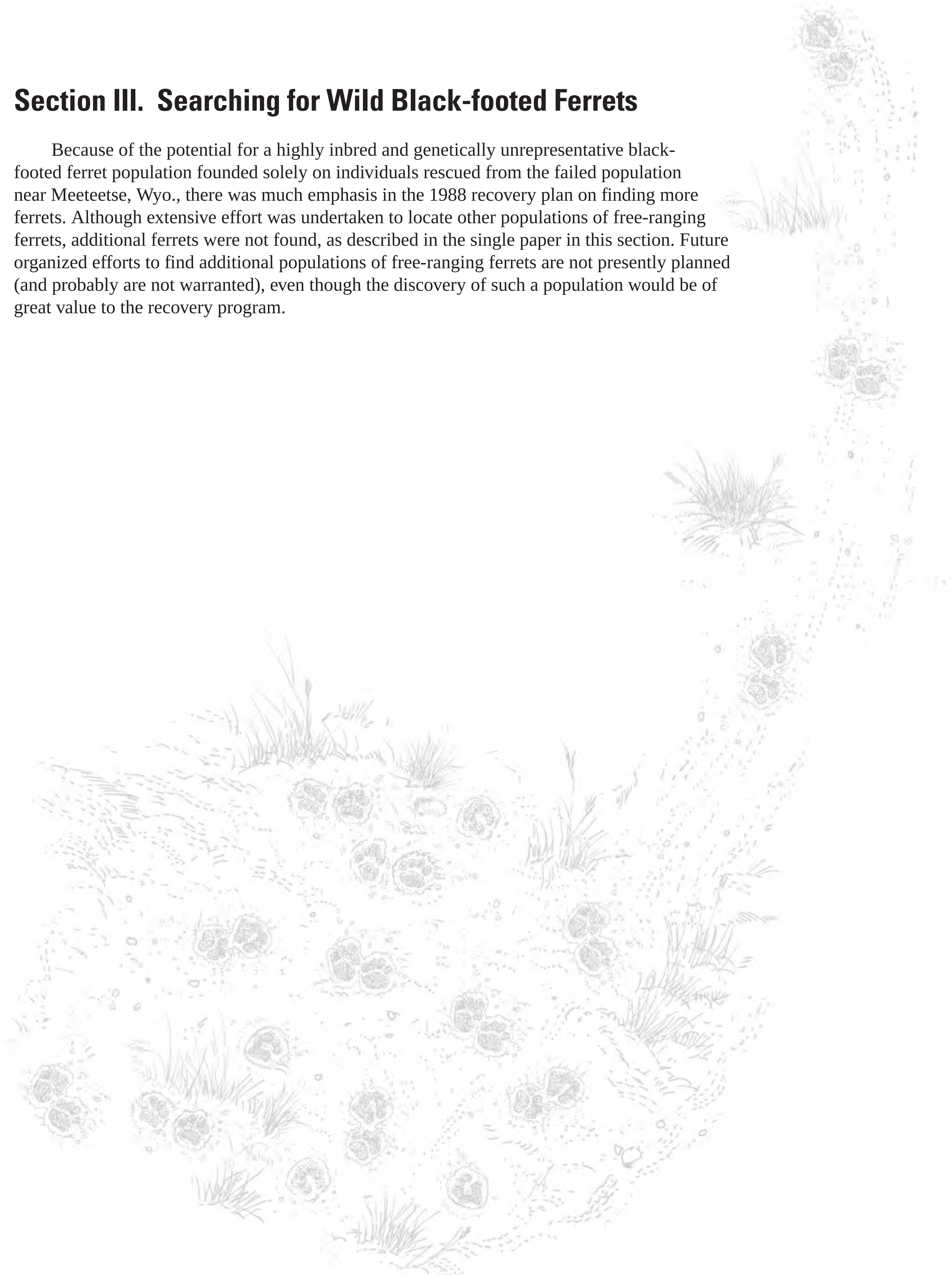
Wisely, S.M., McDonald, D.B., and Buskirk, S.W., 2003, Evaluation of the species survival plan and captive breeding program for the black-footed ferret: Zoo Biology, v. 22, p. 287–298.

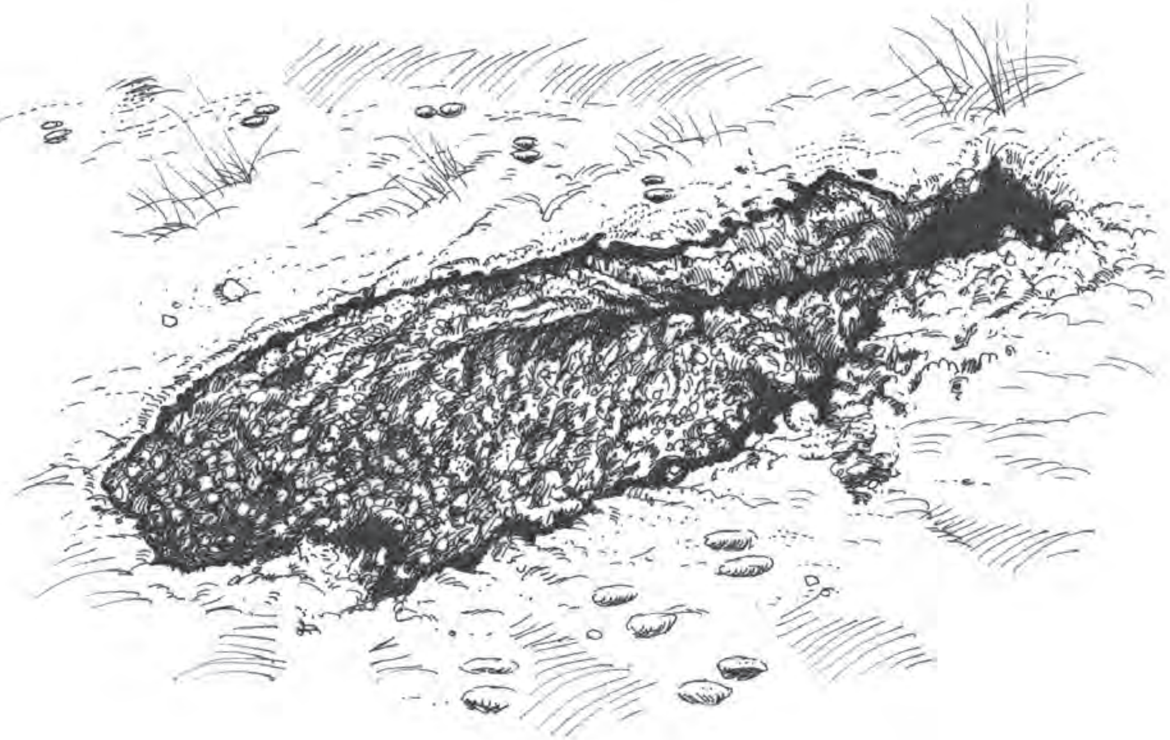
Youngman, P.M., 1994, Beringian ferrets—mummies, biogeography, and systematics: Journal of Mammalogy, v. 75, p. 454–461.



Section III. Searching for Wild Black-footed Ferrets

Because of the potential for a highly inbred and genetically unrepresentative black-footed ferret population founded solely on individuals rescued from the failed population near Meeteetse, Wyo., there was much emphasis in the 1988 recovery plan on finding more ferrets. Although extensive effort was undertaken to locate other populations of free-ranging ferrets, additional ferrets were not found, as described in the single paper in this section. Future organized efforts to find additional populations of free-ranging ferrets are not presently planned (and probably are not warranted), even though the discovery of such a population would be of great value to the recovery program.





A History of Searches for Black-footed Ferrets

By Louis R. Hanebury[1] and Dean E. Biggins[2]

Abstract

Studies of wild populations of black-footed ferrets (*Mustela nigripes*) in South Dakota in the 1960s, in Wyoming in the 1980s, and of captive-bred ferrets reintroduced to unoccupied habitat in Wyoming, South Dakota, and Montana in the 1990s contributed to our understanding of ferret behavior and improved techniques to find ferret populations. We chronicle the efforts of private, State, and Federal institutions that used these techniques to locate remaining populations of ferrets. During the 1980s, a renewed survey effort and solicitation of new sightings, coupled with a monetary reward program, failed to locate ferrets. We believe that the probability of finding ferrets from noncaptive stock is already small and diminishes with each passing year.

Keywords: black-footed ferret, *Mustela nigripes*, reward, sighting, spotlighting, survey technique

Introduction

The original recovery plan for the endangered black-footed ferret (*Mustela nigripes*) was approved in June 1978, and a revised recovery plan was approved in August 1988 (U.S. Fish and Wildlife Service, 1978, 1988). These plans established objectives and outlined steps for recovery that would provide for viable black-footed ferret populations in captivity and in the wild throughout the historical range. A common element in both plans was locating additional wild populations both for preservation and as a source of genetic diversity for the captive population. Brussard and Gilpin (1989) believed that any ferret still extant in the wild should be captured to augment the gene pool available to the captive breeding program. In addition, a multitude of individuals and organizations began work on delineating the historical range of the black-footed ferret, defining and identifying suitable habitat, and developing methodologies and techniques to find remaining populations. This paper presents an overview and update on efforts to locate an undiscovered population of ferrets.

Techniques for Finding a Wild Population of Ferrets

Methodologies to locate black-footed ferrets were first developed during the 11 years (1964–74) that a South Dakota population was studied (Hillman, 1968a,b; Sheets, 1970; Fortenbery, 1972; Hillman and Linder, 1973). Henderson and others (1969) presented important life history and behavioral characteristics, in addition to techniques for studying and locating black-footed ferrets. Nevertheless, Hillman and Linder (1973) emphasized the need to develop more efficient and conclusive techniques for detecting the presence of ferrets on prairie dog (*Cynomys* spp.) towns.

After the South Dakota population disappeared (the last wild ferrets in South Dakota were trapped in 1973; Carpenter and Hillman, 1978), the U.S. Fish and Wildlife Service's (FWS) Denver Wildlife Research Center (DWRC), Section of Wildlife Ecology on Public Lands, conducted black-footed ferret surveys on Federal lands (Martin and Schroeder, 1979, 1980; Smith and others, 1982; Martin, 1983). The objectives of those activities were to search for black-footed ferrets and test new or alternative methods for their detection. These methods included searches for sign (i.e., diggings, tracks, bones, scat, plugged burrows) by foot, horseback, snowmobile, and aircraft during daylight hours, as well as searches for ferrets at night using spotlights (on foot and from vehicles). Other techniques involved observing prairie dog behavior, using night vision equipment, and using scent dogs. A partial listing of such searches conducted by DWRC in Wyoming revealed a total of 1,166 person-hours of night searches with spotlights and much more time spent in day searches. Spotlight searches resulted in sightings of 54 coyotes (*Canis latrans*), 168 badgers (*Taxidea taxus*), and 15 long-tailed weasels (*Mustela frenata*), but there were no sightings of ferrets.

In 1981, a new population of black-footed ferrets was discovered near Meeteetse, Wyo. (Schroeder and Martin,

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1982). Four years of studies by FWS, Biota Research and Consulting, Inc., and the Wyoming Game and Fish Department increased our knowledge about locating and monitoring black-footed ferrets (Biggins, 1983; Biggins and Fagerstone, 1983; Clark and others, 1984b, 1986, 1988; Anderson and Inkley, 1985; Campbell and others, 1985; Clark, 1985; Richardson and others, 1985, 1987; Biggins and others, 1986; Fagerstone and Biggins, 1986; Johnson and others, 1986; Morkill, 1987). Although Clark and Campbell (1981a) had already devised ferret search guidelines, information from the Meeteetse studies assisted in formulating updated search techniques (Clark and others, 1984a, 1988). It also enabled FWS to develop black-footed ferret survey guidelines for compliance with the Endangered Species Act (ESA) of 1973, as amended (16 U.S.C. 1531–1543) (Schroeder, 1985; U.S. Fish and Wildlife Service, 1986). The Wyoming Cooperative Fish and Wildlife Research Unit, in cooperation with FWS, initiated workshops on black-footed ferret survey techniques in 1987. These workshops demonstrated the most current methodology for finding ferret populations. Training and certification were necessary to promote uniformity in techniques used by consultants and agency personnel. Workshops were held periodically until 1994, when Badlands National Park in South Dakota hosted the final training course. Today, skills to survey for black-footed ferrets are developed by individuals participating in field work at one of the active reintroduction sites in six States and in Mexico.

Guidelines were prepared by FWS to locate at least one animal of a population within three consecutive nights of spotlight surveys in a portion of the habitat. Using these survey guidelines (U.S. Fish and Wildlife Service, 1986), the probability of detecting ferrets was found to be high under simulated field conditions (Lindzey and Marinari, 1992; Marinari, 1992). Unpublished data from spotlight surveys for the reintroduced population of black-footed ferrets studied in the mid-1990s on the UL Bend National Wildlife Refuge in Montana confirmed the effectiveness of spotlight surveys using the FWS protocol (R. Matchett, oral commun., 2003). Spotlight surveys conducted while telemetry crews were monitoring radio-tagged ferrets suggested that over 90 percent of the ferrets above ground (as indicated by telemetry) were observed by search crews. Similarly, analysis of ferret observations over a 10-year period in the same area suggested high detectability of ferrets, given adequate search effort (Biggins, Godbey, Matchett, and others, this volume).

Henderson and others (1969) first proposed the use of a helicopter or airplane to locate ferrets during winter. Martin and Schroeder (1980) tested both fixed-wing aircraft and a helicopter for winter surveys to locate ferret sign. They found helicopters more practical because badger diggings were more easily found from helicopters. Biggins and Engeman (1986) found fixed-wing aircraft acceptable for locating ferret sign in winter. Aerial ferret surveys from helicopters were used effectively to survey the large white-tailed prairie dog (*C. leucurus*) complex in northwest Colorado and northeast Utah (U.S. Fish and Wildlife Service, 1989). Aerial surveys with helicopters or fixed-wing aircraft are currently used at some reintroduction sites and have been used successfully to locate ferrets that have dispersed into outlying prairie dog colonies (R. Matchett, oral commun., 2003).

In 1978, the DWRC began testing the use of scent dogs to locate black-footed ferrets or their sign (Conway and Dean, 1979; Southwest Research Institute, 1979; Martin and Schroeder, 1980). Two dogs were trained with scat obtained from captive black-footed ferrets held at FWS's (now U.S. Geological Survey's) Patuxent Wildlife Research Center in Laurel, Md. These dogs were later tested at Meeteetse, Wyo., in 1981 and demonstrated the ability to identify burrows known to be occupied by ferrets. Matchett and Smith (2001) successfully located reintroduced ferrets in Montana with trained scent dogs. Reindl (2004) proposed further testing and use of scent dogs in locating black-footed ferrets dispersing from reintroduction sites. Although variability of individual scent dog performance remains a problem, these studies indicate that dogs may be a useful supplement to spotlight surveys, particularly at sites where conventional search efficiency is poor. For example, scent dogs will be used during 2005 in remote, hard-to-search areas of the Colorado/Utah black-footed ferret reintroduction site (S. Reindl, oral commun., 2004).

Before the discovery of the Meeteetse population, Clark and Campbell (1983) tested a track station survey method using a variety of lures to detect nocturnal mammalian carnivores. Hammer and Anderson (1985) further studied the usefulness of track stations and numerous attractants to determine whether black-footed ferrets were present. Tracking and camera stations did not record any visitation in areas occupied by ferrets in the Meeteetse habitat. Scent stations were tested in ferret-occupied habitat in South Dakota with similar results (T. Livieri, oral commun., 2005). Scent attractants, track stations, and remote cameras have not been proven effective for locating ferrets in the wild.

Weasel-like scats have been collected during nocturnal and daylight surveys for ferrets and ferret sign (Henderson and others, 1969; Fortenbery, 1972; Martin and Schroeder, 1979; Clark and others, 1984a, 1988; Richardson and others, 1987). Typical black-footed ferret scat has been described, but identification of mustelid scat to species is often problematic. Johnson and others (1986) compared the fecal bile acid characteristics of known black-footed ferret scat and other known small carnivores and concluded that these acids did not enable positive identification of individual ferret scats. They did, however, suggest that ferret scats might be identifiable with reasonable confidence using gas-liquid chromatography, a technique yet to be thoroughly tested. Recent advances in DNA testing may provide a reliable and practical method to identify black-footed ferret scats where other sign is not discernible.

Reintroduced black-footed ferrets afforded renewed opportunities to gain knowledge on ferret behaviors, thereby increasing our ability to detect free-ranging ferrets. The first reintroduction of captive-raised black-footed ferrets at Shirley Basin, Wyo., yielded much information regarding behavior, dispersal, and postrelease survival (U.S. Fish and Wildlife Service, 1992; Wyoming Game and Fish Department, 1992, 1993, 1994, 1995; Oldemeyer and others, 1993). Subsequent reintroductions in South Dakota, Montana, Arizona, Colorado, and Utah have each added new data, which collectively have contributed to validating and refining effective search techniques.

Historical Sighting Reports and Surveys

Anderson and others (1986) provided an exhaustive summary of black-footed ferret specimens from North America, beginning with the first specimen collected by Audubon and Bachman in 1851. One of the earliest efforts to solicit black-footed ferret sightings occurred in 1952 (Cahalane, 1954). During the period 1946–53, 42 black-footed ferrets were reported from 42 localities, mostly in South Dakota, Montana, Nebraska, and Colorado (Cahalane, 1954). About one-third of the animals observed were found dead or were trapped (killed), shot, hit by vehicles, or died in captivity.

Cahalane's (1954) call for a life history study of the black-footed ferret was answered in 1964 with the discovery of the population in Mellette County, S. Dak. Before the South Dakota population disappeared, a black-footed ferret and prairie dog workshop in 1973 brought together State, Federal, and academic interests to present historical and current knowledge on prairie dogs and black-footed ferrets (Linder and Hillman, 1973). Eleven States, Federal agencies, and academic institutions provided information on available habitat, historical and recent black-footed ferret sightings, and efforts to locate additional populations (Clark, 1973; Grondahl, 1973; Henderson and Little, 1973; Lewis, 1973; Lewis and Hassien, 1973; Locke, 1973).

Kansas was one of the first States to have an active "Wanted: Black-footed Ferret" program. Historical ferret sightings, ferret specimen records, and new sighting reports formed the foundation for actively looking for additional populations (Henderson and Little, 1973). Letters and pamphlets were widely disseminated, supported by articles in local newspapers and magazines and by public radio and television announcements (Henderson, 1969). A color "Wanted Alive" poster was later produced and sent to all States within the original range of the black-footed ferret (appendix, fig. A1). Clark (1973, 1978, 1980) and Clark and Campbell (1981b) took a similar approach in Wyoming, identifying habitat and gathering historical and new specimen records and sighting reports. Campbell (1989) described searches to locate black-footed ferret populations conducted in Montana between 1984 and 1989. Crete (1985) discussed FWS's efforts to work with State agencies and private entities to find other wild populations of ferrets. A second major black-footed ferret workshop was held in 1984 in Laramie, Wyo. Federal and State agencies summarized new efforts to handle black-footed ferret sighting reports (Cada, 1985; Grode, 1985; Hammer, 1985; Hasenyager, 1985; Lengkeek, 1985).

Because of funding constraints and the lack of any legal mandate, searches for remaining populations of black-footed ferrets were at times limited. For example, despite the black-footed ferret's inclusion in the first list of rare and endangered wildlife by the U.S. Department of the Interior in 1964 (Clark, 1989), in the 1966 Endangered Species Preservation Act, and in the Endangered Species Conservation Act of 1969, there were no prohibitions of harm to a listed species ("taking" was prohibited only within national wildlife refuges) and therefore no requirements to determine whether black-footed ferrets were present prior to authorizing projects that might harm ferrets or modify their habitat. By 1965, the Department of the Interior had established a policy on precontrol surveys for prairie dog control programs throughout the range of the black-footed ferret on all classes of land (Berryman and Johnson, 1973). This policy was initially for, and first applied to, prairie dog control programs on Pine Ridge Indian Reservation in South Dakota (Hanson, 1988, 1993). New Mexico also initiated precontrol surveys for black-footed ferrets during that time (Hubbard and Schmitt, 1983). The policy on precontrol surveys was further refined by Executive Order 11643 (Berryman and Johnson, 1973). Jobman and Anderson (1985) reviewed other Federal authorities that might affect or be used in locating funds or facilitating ferret recovery activities. Schroeder (1988), however, noted the requirement for ferret surveys that was triggered by the ESA of 1973. Under section 7(a)(2), Federal agencies are required to consult with FWS to ensure that any action they authorize, fund, or carry out is not likely to jeopardize the continued existence of any endangered or threatened species or result in the destruction or adverse modification of a species' designated critical habitat. If suitable habitat (i.e., capable of supporting at least one black-footed ferret) is present within the action area, FWS has the authority to recommend that a ferret survey precede the project. In 1986, to provide some consistency in survey recommendations, FWS developed standard survey guidelines (Schroeder, 1985; U.S. Fish and Wildlife Service, 1986). When properly implemented, the prescribed strategy has good potential to detect a population of black-footed ferrets. Validating whether suitable habitat is occupied by ferrets is necessary to determine if an action may adversely affect the species. Because of the policy to include precontrol surveys for black-footed ferrets after 1965, the mandatory consultation requirements for Federal agencies in the ESA of 1973, and pesticide registration label statements (U.S. Environmental Protection Agency, 1987), surveys for black-footed ferrets by Federal agencies and their consultants have been occurring for 40 years. Black-footed ferret populations could have escaped detection because some surveys were inadequate or because some suitable habitats were never surveyed. Nonetheless, these surveys have covered large areas without finding a population of living ferrets (but they have resulted in discovery of old black-footed ferret remains).

In the initial black-footed ferret recovery plan (U.S. Fish and Wildlife Service, 1978), one recovery task was to map the amount of prairie dog habitat occupied by black-footed ferrets, to be accomplished by compiling sighting reports for each State within the historical range (Jobman and Anderson, 1981a). The FWS's Pierre, S. Dak., office was designated as the receiving station for all black-footed ferret sightings; this responsibility was moved to Grand Island, Nebr., in 1985. A questionnaire and letter requesting ferret sightings between January 1, 1970, and January 1, 1981, were sent to Provincial (Canadian), Federal, State, and private (tribal, industry, conservation, and recreation groups) institutions (Jobman and Anderson, 1981b), resulting in reports of 228 sightings. Sightings were classified as confirmed, probable, or unconfirmed. Periodic updates (W. Jobman, written commun., 1987–92) to the original report added the following additional sightings: 232 (1987), 51 (1988), 25 (1989), 26 (1990), 31 (1991), and 25 (1992). Partly because of the paucity of additional sightings, updates were discontinued in 1992, and sighting records are no longer formally maintained by FWS. Individual State or FWS offices may maintain records, however.

There are six reintroduced populations of black-footed ferrets that are designated nonessential, experimental in accordance with section 10(j) of the ESA. The black-footed ferret reintroduction sites represented the best habitat available and would seem to have been likely places to find any extant ferret populations. To comply with Section 10(j), all of these release sites were surveyed for resident black-footed ferrets. For example, there were 350 black-footed ferret surveys conducted on lands occupied by prairie dogs at the first site designated (Shirley Basin/Medicine Bow, Wyo.) to receive black-footed ferrets in 1991 (U.S. Fish and Wildlife Service, 1991). Other areas designated as nonessential, experimental populations received similar search efforts (U.S. Fish and Wildlife Service, 1993, 1994, 1996, 1998). Resident populations of ferrets were not found in any of the six areas.

Early Reward Programs

Throughout the 1970s, many States within the historical range of the black-footed ferret solicited sightings of ferrets. In 1974, Dr. Tim Clark, through an effort funded by the National Geographic Society and the National Academy of Sciences, solicited sightings from Wyoming and all States within the historical range of the black-footed ferret (Campbell, 1989). Clark went a step further by offering a $50 reward for a photograph or other information leading to the discovery of ferrets in the wild. "Wanted" posters (appendix, fig. A2) were widely distributed, and the reward was increased to $250 in 1980.

Other States, such as Oklahoma (Hassien, 1976) and New Mexico (Hubbard and Schmitt, 1983), had active publicity programs to solicit sighting reports of black-footed ferrets. The New Mexico Department of Game and Fish during 1978–81 and the New Mexico State Office of the Bureau of Land Management in 1982 conducted well-organized campaigns to solicit black-footed ferret sightings (Hubbard and Schmitt, 1983). The program was well publicized through posters, postcards, newspapers, magazines, and television. None of the 78 records produced was considered reliable evidence for the continued existence of black-footed ferrets in New Mexico (Hubbard and Schmitt, 1983).

Clark's $250 reward was paid to the finders of the Meeteetse, Wyo., ferret that led to the discovery of the last known extant population. Following that seminal event, biologists developed a program to locate ferrets in Montana by offering a monetary reward (Campbell, 1989). In 1983, Montana Fish, Wildlife and Parks and Biota Research and Consulting, Inc., developed a reporting system designed to standardize and assess ferret sightings, presenting criteria to evaluate each sighting and a protocol to follow if ferrets were discovered. The publicity resulted in 69 ferret reports by August 1986, but none resulted in locating and capturing a live black-footed ferret. In August 1986, Montana Fish, Wildlife and Parks initiated a new program soliciting ferret sightings but now offering a monetary reward (Flath, 1987). It included a mailer (appendix, fig. A3) describing the reward program and a standardized reporting form (appendix, fig. A3). A $5,000 reward for information leading to the discovery of a wild population of black-footed ferrets in Montana was offered by Wildlife Conservation International (a subsidiary of the New York Zoological Society). This program not only offered a significant reward but also made it the responsibility of the person submitting the sighting to include adequate information, limiting the need for follow-up on reports that were questionable. The reward program was aggressively advertised and included the distribution of "Wanted" posters (appendix, fig. A4) in post offices, public buildings, and businesses. The monetary reward program generated 66 additional responses (Campbell, 1989), but none led to the discovery of additional ferrets.

Recovery Activities at the National Ecology Research Center

In 1988, FWS approved a revised black-footed ferret recovery plan (U.S. Fish and Wildlife Service, 1988). The FWS's National Ecology Research Center (NERC; now the U.S. Geological Survey's Fort Collins Science Center) was responsible for completion of many of the revised recovery tasks outlined in the plan. One of these tasks was finding additional ferrets to bolster the depauperate genetic representation of ferrets in the captive breeding program. Biggins and Crete (1989), Hanebury and Biggins (1989), and Godbey and Biggins (1994) discussed FWS activities associated with finding ferrets under the new Black-footed Ferret Recovery

Plan. To locate additional ferrets, NERC expanded Montana's black-footed ferret reward program to other States and renewed black-footed ferret surveys on the best remaining ferret habitat.

National Reward Program

The Black-footed Ferret Interstate Coordinating Committee (ICC) was established in 1987 to improve communication and promote ferret recovery in 12 States, two Canadian Provinces, and the State of Chihuahua, Mexico. In 1987, the ICC identified the need for a national reward program and recommended a program similar to that used by Montana. In the fall of 1987, Wildlife Conservation International agreed to apply its $5,000 reward to any State within the former range of the black-footed ferret that wished to participate. States in the program had to be prepared to follow up on all reported sightings within a reasonable amount of time. Montana, Wyoming, Colorado, South Dakota, Utah, Nebraska, Oklahoma, Texas, and Arizona participated in the program. The Navajo Nation, encompassing a large area in both New Mexico and Arizona, also joined the effort. A new poster applicable to all States offering the $5,000 reward was prepared, and by February 1988, 10,000 copies were distributed. The revised posters (appendix, fig. A5) included a photo of a distinctive ferret-digging on snow and sketches of ferret tracks; to qualify for the reward, the observer needed to submit a photograph or information that resulted in verification of one or more live black-footed ferrets. To increase the quality and quantity of responses, Wildlife Conservation International agreed to increase the reward to $10,000 (appendix, fig. A6), effective March 3, 1989. Thousands of updated $10,000 reward posters were mailed to participating States.

New black-footed ferret sighting report forms were developed, incorporating the knowledge gathered from studying the Meeteetse population and experience gained from earlier ferret surveys in response to sighting reports. Ranking criteria and instructions were also developed. A sighting report was scored as highly probable, likely, fair, or unlikely. Such a classification was intended to limit follow-up investigations to the most probable sightings. This conservative approach addressed concerns about "probable" and "confirmed" sighting classifications used by Jobman and Anderson (1981a,b). They defined a probable sighting as one made by a qualified observer or a competent observer who was not positive about a sighting. A confirmed sighting was defined as one made by a competent and dependable observer who had no doubts that the animal seen was a black-footed ferret observed in or near suitable habitat (Jobman and Anderson, 1981a,b).

As part of the national reward program, an extensive effort was made to advertise the reward through all forms of local, statewide, and national media. The communications division of the Wyoming Game and Fish Department assisted NERC in producing audio and video public service announcements on the reward offer, which were sent to radio and television stations. Press releases describing summer and winter ferret behavior and sign, along with the posters, were distributed to the print media. Articles on the black-footed ferret reward program appeared in local and major newspapers and magazines. Major networks ran segments on programs such as *Missing: Reward* and NBC's *Today Show*, and special presentations such as the British Broadcasting Corporation's "Wildlife On One: Wanted Alive," which aired on *National Geographic Explorer*.

Responses to the reward program are difficult to quantify because each State handled incoming reports independently. Reports came directly to NERC or were forwarded from the receiving States. Although respondents provided descriptive photographs, drawings, and detailed characteristics, the photographs typically were of domestic ferrets (*Mustela putorius furo*) from both within and outside the black-footed ferret's historical range (e.g., California, Colorado, Florida, Kentucky, Nevada, Texas, and Utah), as well as photographs of long-tailed and bridled weasels (*Mustela frenata*), badgers, and prairie dogs. Photographs of black-footed ferrets were received from individuals in South Dakota and Alberta, Canada. Both of the photographs matched older photos taken by others, and both reports were judged to be hoaxes. The $10,000 reward offer was terminated on December 31, 1990.

Renewed Search Efforts

During the time of the national reward program, NERC formed black-footed ferret survey teams that were prepared to respond to valid sighting reports and to make one final effort to look for ferrets in suitable habitat. Between 1984 and 1988, six black-footed ferret sightings were reported in or around Waterton Lakes National Park in Alberta, Canada (Laing, 1988). Those reports were investigated in 1989 by Waterton Lakes National Park personnel, a local naturalist, NERC, and FWS personnel (Hanebury, 1989; Harvie, 1989; McGill, 1989). To lend credence to the reports, there were previous specimens or sighting records from Alberta and Saskatchewan (Russell, 1985; Anderson and others, 1986; Laing, 1987; Laing and Holroyd, 1989). In Canada, black-footed ferret surveys before this new effort were limited to those by Millson (1976), Laing (1987), and Laing and Holroyd (1989). Laing and Holroyd (1989) listed 15 recent sightings from 1967 to 1986 and surveyed all reported sites. No black-footed ferrets were confirmed by either the past efforts or the more recent efforts by NERC in and around Waterton Lakes National Park. Highly ranked reports on Navajo Nation lands in New Mexico were also investigated with negative results (Hanebury, 1988a). A brief search (26 person-hours) in the largest black-tailed prairie dog complex in North America, in Chihuahua, Mexico (Ceballos and others, 1993), did not detect any black-footed ferrets (Hanebury, 1988b), but there were 33 sightings of coyotes and 4 sightings of badgers. A partial tally of accessible data revealed 978 person-hours of spotlight searches conducted by NERC personnel in response to range-wide ferret sighting reports. The searches resulted in sightings of many other predators, including 187 coyotes, 193 badgers, and 17 long-tailed weasels, but the widely advertised $10,000 reward and subsequent investigations produced no proof of free-ranging ferrets.

In addition to responding to the sighting reports, NERC survey crews directed efforts to the locations that seemed most likely to harbor ferrets as determined by specimen records, clustered sighting reports, and information suggesting the presence of high-quality habitat (Jobman and Anderson, 1981b; Anderson and others, 1986; W. Jobman, written commun., 1984, 1992). These areas were located in South Dakota, Montana, and Wyoming. In the mid-1970s, when no remaining South Dakota ferret populations could be found, searches throughout the historical range of the black-footed ferret were undertaken by State resource agencies, private consultants, industry, university students, private citizens, and Federal agency biologists. Because no centralized repository for black-footed ferret survey data existed, it is impossible to quantify the hours devoted to spotlighting for ferrets, the area covered, or how many times the same area was searched through time.

Other evidence of a declining black-footed ferret population includes the number of ferret specimens obtained from poisoning, trapping, vehicle collisions, or other sources. Peak numbers occurred during the 1920s and 1930s (fig. 1), perhaps the period when the largest areas of prairie dog colonies were poisoned. Biggins and Schroeder (1988) speculated that this increase probably reflected increased attention given the species rather than a change in the population. No specimens were retrieved during the late 1970s and early 1980s. Although trapping probably decreased during that time, vehicular traffic and miles of roads increased. Cahalane (1954) reported that out of 42 sighting records from the period 1946–53, 17 ferrets were killed before or after the sighting. Four of those deaths were road kills between 1948 and 1953. During studies of the ferret population in south-central South Dakota in Mellette County, eight road-killed ferrets were documented in about 8 years (Hillman and Linder, 1973). There were no reported ferret road kills during the decade of the 1980s. It was not until 1994, after captive-bred black-footed ferrets were reintroduced to unoccupied habitat, that ferret specimens again began to be collected as road kills (fig. 1).

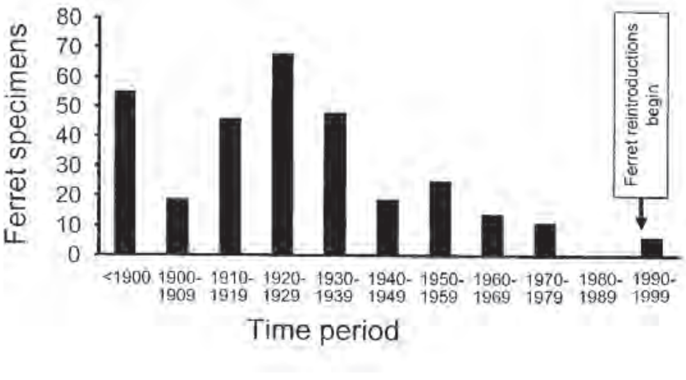


Figure 1. Number of black-footed ferret (*Mustela nigripes*) specimens collected by decade from Anderson and others (1986) and Clark (1989), including the decade after ferret reintroductions.

Summary

Since the decline of the last known ferret population in South Dakota, substantial effort has been devoted to identifying viable ferret habitat and locating any remaining isolated ferret populations. Survey techniques were developed and used as a reliable standard to find black-footed ferrets. Search efforts increased after the establishment of a policy for prairie dog precontrol surveys in 1965 and following implementation of the ESA in FWS field offices throughout the historical range of the ferret. None of the searches performed to implement recovery plan tasks, to comply with ESA section 7 consultation requirements (including pesticide registration), and to ensure compliance with the “take” prohibitions of section 9 of the ESA, nor heroic efforts by private individuals and conservation groups, have found any black-footed ferrets in the wild. At some locations, the lack of success in finding wild ferrets, combined with the desire by some agencies and organizations to expedite projects (e.g., prairie dog control, oil and gas development) in ferret habitat (i.e., prairie dog colonies), has resulted in requests for FWS to declare areas entirely “ferret free” (i.e., to “block-clear” the area from the need for preproject ferret searches) (Campbell and others, 1990). Today, requirements for preproject ferret surveys have been either officially eliminated or deemphasized in all of the 12 States composing the historical range of the black-footed ferret. The majority of the ferret range in South Dakota has been either block-cleared or exempted from the need for ferret surveys because of designation of experimental areas for ferret reintroduction through deliberative processes (South Dakota Department of Agriculture and South Dakota Department of Game, Fish and Parks, 2003). Other States with significant remaining areas of viable ferret habitat (active prairie dog colonies) have officially block-cleared habitat not considered valuable for ferret recovery (Colorado, R. Krueger, oral commun., 2005; Wyoming, M. Jennings, written commun., 2004). For the most part, North Dakota (B. Bicknell, oral commun., 2005), Nebraska (B. Harms, oral commun., 2005), Kansas (D. Mulhern, oral commun., 2005), Oklahoma (S. Harmon, oral commun., 2005), Utah (R. Chi, oral commun., 2005), and Texas (J. Hughs, oral commun., 2005) do not require preproject ferret surveys for section 7 consultation. New Mexico considers the black-footed ferret to be extirpated and therefore does not require preproject surveys (M. Murphy, oral commun., 2005).

Some organizations have promoted block-clearing as a strategy to improve public sentiment toward black-footed ferret recovery and prairie dog conservation (Patton and

Leachman, 1991). Further, the now widely held view that the probability of ferrets persisting in the wild is low, combined with the expense of conducting guideline-standard ferret searches, has caused FWS to relax section 7 consultation requirements (M. Lockhart, written commun., 2003) and propose that tasks relating to additional ferret searches be deemphasized in a second revision of the black-footed ferret recovery plan (U.S. Fish and Wildlife Service, 2004). A review of ferret survey needs is still in progress, however, and will be reflected in the final revised recovery plan.

Over 15 years ago, Lacy and Clark (1989) examined genetic variability in black-footed ferret populations and stated that it was unlikely that a long-term viable population of ferrets existed in the wild. We believe that the probability of finding ferrets that stem from noncaptive stock is already small and diminishes with each passing year. There are, however, several remaining considerations. With the reintroduction of over 1,900 captive-raised black-footed ferrets and with much recruitment of wild-born kits since 1991, the possibility of newly established populations in the wild will increase. The example of the remarkable persistence of ferrets in the disease-prone, vast, but fragmented habitat of Shirley Basin, Wyo. (Grenier and others, 2004), gives us hope that free-ranging ferrets will persist in other States as reintroductions continue. In addition to the need to monitor reestablished ferret populations, there will be a continued need for improved monitoring methodologies and searches to locate future populations established by dispersing young.

References Cited

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Anderson, S.H., and Inkley, D.B., eds., 1985, Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 1.1–33.12.

Berryman, J.H., and Johnson, N.C., 1973, Ferret and prairie dog programs on public lands—a perspective and some facts, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 109–125.

Biggins, D., 1983, Movements and activity patterns of radio-tagged black-footed ferrets: U.S. Fish and Wildlife Service Summary Report, 48 p.

Biggins, D.E., and Crete, R.A., 1989, Black-footed ferret recovery, *in* Bjugstad, A.J., Uresk, D.W., and Hamre, R.H., technical coordinators, Ninth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-171, p. 59–63.

Biggins, D.E., and Engeman, R.E., 1986, Aerial survey for black-footed ferret sign in snow, *in* Abstracts of contributed papers, 13th International Biometrics Conference, Seattle, Wash.: Washington, D.C., International Biometrics Society, p. 7.2.

Biggins, D.E., and Fagerstone, K.A., 1983, Black-footed ferret research, Meeteetse, Wyoming: Fort Collins, Colo., U.S. Fish and Wildlife Service, Denver Wildlife Research Center, 5 p.

Biggins, D.E., and Schroeder, M.H., 1988, Historical and present status of the black-footed ferret, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 93–97.

Biggins, D.E., Schroeder, M.H., Forrest, S.C., and Richardson, L., 1986, Activity of radio-tagged black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 135–140.

Brussard, P.F., and Gilpin, M.E., 1989, Demographic and genetic problems of small populations, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 37–48.

Cada, J.D., 1985, Montana’s role in ferret management and handling of ferret sightings, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 14.1–14.7.

Cahalane, V.H., 1954, Status of the black-footed ferret: Journal of Mammalogy, v. 35, p. 418–424.

Campbell, T.M., III, 1989, Prairie dog colony location surveys and black-footed ferret searches in Montana, *in* Clark, T.W., Hinckley, D., and Rich, T., eds., The prairie dog ecosystem—managing for biological diversity: Billings, Montana BLM Wildlife Technical Bulletin No. 2., p. 1–12.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Campbell, T.M., III, Crete, R., and Leachman, R., 1990, Strategy for block clearance of prairie dog colonies and complexes (draft): Denver, Colo., U.S. Fish and Wildlife Service, 14 p.

Carpenter, J.W., and Hillman, C.N., 1978, Husbandry, reproduction, and veterinary care of captive ferrets: American Association of Zoo Veterinarians, Annual Proceedings, p. 36–47.

Ceballos, G., Mellink, E., and Hanebury, L.R., 1993, Distribution and conservation status of prairie dogs *Cynomys mexicanus* and *Cynomys ludovicianus* in Mexico: Biological Conservation, v. 63, p. 105–112.

Clark, T.W., 1973, Prairie dogs and black-footed ferrets in Wyoming, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 88–101.

Clark, T.W., 1978, Current status of the black-footed ferret in Wyoming: Journal of Wildlife Management, v. 42, p. 128–134.

Clark, T.W., 1980, A listing of reports of black-footed ferrets in Wyoming (1851–1977): Northwest Science, v. 54, p. 47–54.

Clark, T.W., 1985, Black-footed ferret studies in Wyoming: National Geographic Society Research Reports, v. 18, p. 223–231.

Clark, T.W., 1989, Conservation biology of the black-footed ferret, *Mustela nigripes*: Philadelphia, Wildlife Preservation Trust International, Special Scientific Report No. 3, 175 p.

Clark, T.W., and Campbell, T.M., III, 1981a, Suggested guidelines for black-footed ferret surveys: Jackson, Wyo., Biota Research and Consulting, Inc., 7 p.

Clark, T.W., and Campbell, T.M., III, 1981b, Additional black-footed ferret (*Mustela nigripes*) reports from Wyoming: Great Basin Naturalist, v. 41, p. 360–361.

Clark, T.W., and Campbell, T.M., III, 1983, A small carnivore survey technique: Great Basin Naturalist, v. 43, p. 438–440.

Clark, T.W., Campbell, T.M., III, Schroeder, M.H., and Richardson, L., 1984a, Handbook of methods for locating black-footed ferrets: Cheyenne, Wyoming BLM Technical Bulletin No. 1, 55 p.

Clark, T.W., Campbell, T.M., III, Schroeder, M.H., and Richardson, L., 1988, Handbook of methods for locating black-footed ferrets: Cheyenne, Wyoming BLM Technical Bulletin No. 1, 61 p.

Clark, T.W., Richardson, L., Casey, D., Campbell, T.M., III, and Forrest, S.C., 1984b, Seasonality of black-footed ferret diggings and prairie dog burrow plugging: Journal of Wildlife Management, v. 48, p. 1441–1444.

Clark, T.W., Richardson, L., Forrest, S.C., Casey, D.E., and Campbell, T.M., III, 1986, Descriptive ethology and activity patterns of black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 115–134.

Conway, M.C., and Dean, E.E., 1979, Endangered species: dog training for black-footed ferret detection: New Mexico Department of Game and Fish, project no. N.M. E-001-R-01.

Crete, R., 1985, Current activities of the U.S. Fish and Wildlife Service in black-footed ferret recovery management, *in* Anderson, S.H., and Inkley, D.B, eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 15.1–15.6.

Fagerstone, K.A., and Biggins, D.E., 1986, Summary of black-footed ferret and related research conducted by the Denver Wildlife Research Center, 1981–1985: Denver, Colo., U.S. Fish and Wildlife Service, Denver Wildlife Research Center, 31 p.

Flath, D., 1987, Wanted: the masked stranger: Montana Outdoors, v. 18, p. 18–22.

Fortenbery, D.K., 1972, Characteristics of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Resource Publication 109, 8 p.

Godbey, J., and Biggins, D., 1994, Recovery of the black-footed ferret—looking back, looking forward: Endangered Species Technical Bulletin, v. 19, p. 10–13.

Grenier, M., Van Fleet, L., and Oakleaf, B., 2004, Spotlighting for free ranging black-footed ferrets in the Shirley Basin/Medicine Bow Management Area, Wyoming, *in* Cerovski, A.O., ed., Threatened, endangered and nongame bird and mammal investigations: Cheyenne, Wyoming Game and Fish Department, p. 19–35.

Grode, M.R., 1985, The black-footed ferret in Colorado, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 17.1–17.4.

Grondahl, C.R., 1973, Status of the black-tailed prairie dog and black-footed ferret in North Dakota, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 51–60.

Hammer, D.A., 1985, The handling of black-footed ferret sighting reports in Wyoming, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 18.1–18.4.

Hammer, D.A., and Anderson, S.H., 1985, Using scent attractants as a technique to locate black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 26.1–26.12.

Hanebury, L.R., 1988a, Black-footed ferret surveys on Navajo Tribal Lands: Fort Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 14 p.

Hanebury, L.R., 1988b, Black-tailed prairie dog and black-footed ferret investigations in Chihuahua, Mexico: Fort

Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 27 p.

Hanebury, L.R., 1989, Black-footed ferret investigations in Canada—return to Waterton Lakes National Park, Waterton Lakes, Alberta, February 20–23, 1989: Fort Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 4 p.

Hanebury, L.R., and Biggins, D., 1989, Black-footed ferret recovery update: Endangered Species Technical Bulletin, v. 14, p. 10.

Hanson, R., 1988, A chronology of prairie dog control operations and related developments in South Dakota, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 121–122.

Hanson, R., 1993, Control of prairie dogs and related developments in South Dakota, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 5–7.

Harvie, W., 1989, The black-footed ferret frenzy—wildlife lovers search Waterton Park for the elusive species: Alberta Report, May 8, 1989, p. 24.

Hasenyager, R., 1985, Utah's ferret program—past, present and future?, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 19.1–19.2.

Hassien, F.D., 1976, A search for black-footed ferrets in the Oklahoma Panhandle and adjacent areas and an ecological study of the black-tailed prairie dog in Texas County, Oklahoma: Stillwater, Oklahoma State University, M.S. thesis, 111 p.

Henderson, F.R., 1969, Wanted—black-footed ferret: Manhattan, Kansas State University, Cooperative Extension Service, 8 p.

Henderson, F.R., and Little, R.J., 1973, Status of the black-footed ferret and black-tailed prairie dog in Kansas, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 34–44.

Henderson, F.R., Springer, P.F., and Adrian, R., 1969, The black-footed ferret in South Dakota: Pierre, South Dakota Department of Game, Fish, and Parks, Technical Bulletin 4, 37 p.

Hillman, C.N., 1968a, Life history and ecology of the black-footed ferret in the wild: Brookings, South Dakota State University, M.S. thesis, 29 p.

Hillman, C.N., 1968b, Field observations of black-footed ferrets in South Dakota: Transactions of the North American Wildlife and Natural Resources Conference, v. 33, p. 433–443.

Hillman, C.N., and Linder, R.L., 1973, The black-footed ferret, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 10–23.

Hubbard, J.P., and Schmitt, C.G., 1983, The black-footed ferret in New Mexico: Santa Fe, New Mexico Game and Fish Department, 118 p.

Jobman, W.G., and Anderson, M.E., 1981a, Potential present range of the black-footed ferret as of January 1, 1981: Pierre, S. Dak., U.S. Fish and Wildlife Service, 64 p.

Jobman, W.G., and Anderson, M.E., 1981b, Current black-footed ferret range as indicated by questionnaire survey: Pierre, S. Dak., U.S. Fish and Wildlife Service, 32 p.

Jobman, W.G., and Anderson, M.E., 1985, Legal status and required action ferret research and management, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 2.1–2.8.

Johnson, M.K., Clark, T.W., Schroeder, M.H., and Richardson, L., 1986, Fecal bile acids of black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 141–144.

Lacy, R.C., and Clark, T.W., 1989, Genetic variability in black-footed ferret populations—past, present, and future, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 83–103.

Laing, R.I., 1987, The reestablishment of the black-footed ferret to the Canadian prairie, *in* Holroyd, G.L., McGillivray, W.B., Stepney, P.H.R., Ealey, D.M., Trottier, G.C., and Eberhart, K.E., eds., Proceedings of the workshop on endangered species in the Prairie Provinces, January 24–26, 1986: Edmonton, Provincial Museum of Alberta Natural History, Occasional Paper No. 9, p. 293–297.

Laing, R.I., 1988, Black-footed ferret habitat mapping and verification in Waterton Lakes National Park, 1988: Report to Environment Canada, Canadian Park Service, 19 p.

Laing, R.I., and Holroyd, G.L., 1989, The status of the black-footed ferret in Canada: Blue Jay, v. 47, p. 121–125.

Lengkeek, D., 1985, Black-footed ferret program in South Dakota, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 21.1–21.4.

Lewis, J.C., 1973, Additional records of black-footed ferrets in Oklahoma: Southwestern Naturalist, v. 18, p. 350.

Lewis, J.C., and Hassien, F., 1973, Status of prairie dogs and surveys for black-footed ferrets in Oklahoma, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 60–75.

Linder, R.L., and Hillman, C.N., preparers, 1973, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, 208 p.

Lindzey, F., and Marinari, P.E., 1992, Spotlighting for black-footed ferrets: U.S. Fish and Wildlife Service, Research Information Bulletin No. 74, 2 p.

Locke, R.A., 1973, Status of the black-footed ferret and black-tailed prairie dog in Nebraska, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 44–47.

Marinari, P.E., 1992, Detectability of black-footed ferrets using spotlighting: Laramie, University of Wyoming, M.S. thesis, 126 p.

Martin, S.J., 1983, Additional records of black-footed ferrets in Wyoming: Southwestern Naturalist, v. 28, p. 95.

Martin, S.J., and Schroeder, M.H., 1979, Black-footed ferret surveys on seven coal occurrence areas in southwestern and southcentral Wyoming (June to September 1978): Cheyenne, Wyo., final report to the Bureau of Land Management, 37 p.

Martin, S.J., and Schroeder, M.H., 1980, Black-footed ferret surveys on seven coal occurrence areas in Wyoming (February to September 1979): Fort Collins, Colo., U.S. Fish Wildlife Service and Bureau of Land Management, Ferret Report No. 2, 34 p.

Matchett, R., and Smith, D., 2001, Use of dogs for black-footed ferret presence detection—progress report: Lewistown, Mont., Charles M. Russell National Wildlife Refuge, 4 p.

McGill, R.J., 1989, Black-footed ferret—final report for Waterton Lakes National Park: Waterton Lakes, Alberta, Environment Canada, Canadian Park Service, 6 p.

Millson, R., 1976, The black-footed ferret in the proposed Grasslands National Park: University of Calgary, Alberta, Canada, M.S. thesis, 107 p.

Morkill, A., 1987, Black-footed ferret surveys—statewide, completion report, April 15, 1986 to April 14, 1987, *in* Oakleaf, B., Belitsky, D., and Ritter, S., eds., Endangered and nongame bird and mammal investigations, annual completion report: Lander, Wyoming Game and Fish Department, Nongame Program, Biological Services Section, p. 59–68.

Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., 1993, Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, 97 p.

Patton, G., and Leachman, R., 1991, Black-footed ferret habitat evaluation and search project in Northeast Colorado. Final report: Grand Junction, Colo., U.S. Fish and Wildlife Service, 56 p.

Reindl, S.A., 2004, Efficacy of scent dogs in detecting black-footed ferrets (*Mustela nigripes*) at a reintroduction site in South Dakota: Brookings, South Dakota State University, M.S. Thesis, 60 p.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1985, Snow-tracking as a method to search for and study the black-footed ferret, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 25.1–25.11.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming: American Midland Naturalist, v. 117, p. 225–239.

Russell, R.H., 1985, The black-footed ferret in Canada, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 20.1–20.2.

Schroeder, M., 1988, Endangered species considerations in prairie dog management, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 123–124.

Schroeder, M.H., 1985, U.S. Fish and Wildlife Service guidelines for black-footed ferret surveys, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 27.1–27.5.

Schroeder, M.H., and Martin, S., 1982, Search for the black-footed ferret succeeds: Wyoming Wildlife, v. 46, p. 8–9.

Sheets, R.G., 1970, Ecology of the black-footed ferret and the black-tailed prairie dog: Brookings, South Dakota State University, M.S. thesis, 51 p.

Smith, D.W., Hammer, D.A., Schroeder, M.H., and Martin, S.J., 1982, Black-footed ferret surveys on coal occurrence areas in southcentral Wyoming, June–September, 1981. Final report: Fort Collins, Colo., U.S. Fish and Wildlife Service, Denver Wildlife Research Center, 43 p.

South Dakota Department of Agriculture and South Dakota Department of Game, Fish and Parks, 2003, An evaluation of the block clearance process in South Dakota: Pierre, S. Dak., 17 p.

Southwest Research Institute, 1979, Training of dogs to detect black-footed ferrets: San Antonio, Tex., Southwest Research Institute, project report no. 14-5331, 7 p.

U.S. Environmental Protection Agency, 1987, Strychnine; intent to cancel; partial withdrawal of prior cancellation notice: Federal Register, v. 52, p. 6762–6765.

U.S. Fish and Wildlife Service, 1978, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 145 p.

U.S. Fish and Wildlife Service, 1986, Black-footed ferret survey guidelines for compliance with the Endangered Species Act: Denver, Colo., and Albuquerque, N. Mex., U.S. Fish and Wildlife Service, 17 p.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

U.S. Fish and Wildlife Service, 1989, Black-footed ferret search activities, northwest Colorado and Northeast Utah: Golden, Colo., U.S. Fish and Wildlife Service, 49 p.

U.S. Fish and Wildlife Service, 1991, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in southeastern Wyoming: Federal Register, v. 56, p. 23830–23842.

U.S. Fish and Wildlife Service, 1992, Reintroduction of the black-footed ferret *Mustela nigripes*: Fort Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 44 p.

U.S. Fish and Wildlife Service, 1993, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in north-central Montana: Federal Register, v. 58, p. 19220–19231.

U.S. Fish and Wildlife Service, 1994, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in south-western South Dakota: Federal Register, v. 59, p. 42682–42694.

U.S. Fish and Wildlife Service, 1996, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in Aubrey Valley, Arizona: Federal Register, v. 61, p. 11320–11336.

U.S. Fish and Wildlife Service, 1998, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in northwestern Colorado and northeastern Utah: Federal Register, v. 63, p. 52824–52841.

U.S. Fish and Wildlife Service, 2004, Draft black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 136 p.

Wyoming Game and Fish Department, 1992, Black-footed ferret reintroduction in Shirley Basin, Wyoming—1991 annual completion report: Cheyenne, Wyoming Game and Fish Department, 256 p.

Wyoming Game and Fish Department, 1993, Black-footed ferret reintroduction in Shirley Basin, Wyoming—1992 annual completion report: Cheyenne, Wyoming Game and Fish Department, 244 p.

Wyoming Game and Fish Department, 1994, Black-footed ferret reintroduction in Shirley Basin, Wyoming—1993 annual completion report: Cheyenne, Wyoming Game and Fish Department, 94 p.

Wyoming Game and Fish Department, 1995, Black-footed ferret reintroduction in Shirley Basin, Wyoming—1994 annual completion report: Cheyenne, Wyoming Game and Fish Department, 59 p.

Appendix. Posters Used To Solicit Reports of Black-footed Ferret Sightings

WANTED ALIVE

Black Footed Ferrets

and Their Location

Photo—F. Robert Henderson

Size: About 2 feet long including the tail.
Identifying Markings: Black face-mask, black-tipped tail, black feet, body color is yellow-tan.
Habitat: Usually prairie dog towns or near them. May be seen elsewhere when moving between prairie dog towns, during searches for food and during breeding season.
Abundance: One of rarest mammals in North America.

PLEASE, report! (See contact at bottom of poster)

DON'T BE CONFUSED BY THESE ANIMALS THAT LOOK LIKE THE BLACK-FOOTED FERRET

Photo—F. Robert Henderson

European Ferret

Size: About the same as the black-footed ferret.
Identifying Markings: Similar to those of the black-footed ferret, **except,** nose more pointed, more black on tail and the fur is more bushy to give a heavier body appearance. Body color usually appears darker, because of dark-colored guard hairs. Feet **are** black.
Habitat and Abundance: Common laboratory animal and sold in pet shops. Often released to the wild by owners.

Photo—Jon Farrar

Long-Tailed Weasel

Size: About one-half the size of a black-footed ferret.
Identifying Markings: Yellowish-white underparts and black-tipped tail. Body color is reddish-brown. Winter color is white except black-tipped tail. Feet **not** black.
Habitat and Abundance: Can be found on most land habitats where prey species available, and often near water.

Bridled Weasel

Size: About one-half the size of a black-footed ferret.
Identifying Markings: Same as long-tailed weasel only has black face-mask. Feet **not** black.
Habitat and Abundance: Similar to long-tailed weasel. Mostly occurs in Southwestern U.S.

Photo—Ernie Peck

Cooperative Extension Service
Kansas State University
and
The U.S. Department of the Interior
Fish and Wildlife Service

All educational programs and materials are available without discrimination on the basis of race, color, national origin, sex, or handicap.

PLEASE REPORT TO:

Lou Hanebury - National Ecology Center, USFWS
1300 Blue Spruce Drive
Fort Collins, CO 80524
(303) 226-9460 Night (303) 224-2849

Figure A1. The first poster used to solicit information about locations of black-footed ferrets (*Mustela nigripes*) (original poster was in color).

WANTED

DO
NOT
KILL
OR
TRAP

DO
NOT
KILL
OR
TRAP

$50 REWARD

for Photograph & Information

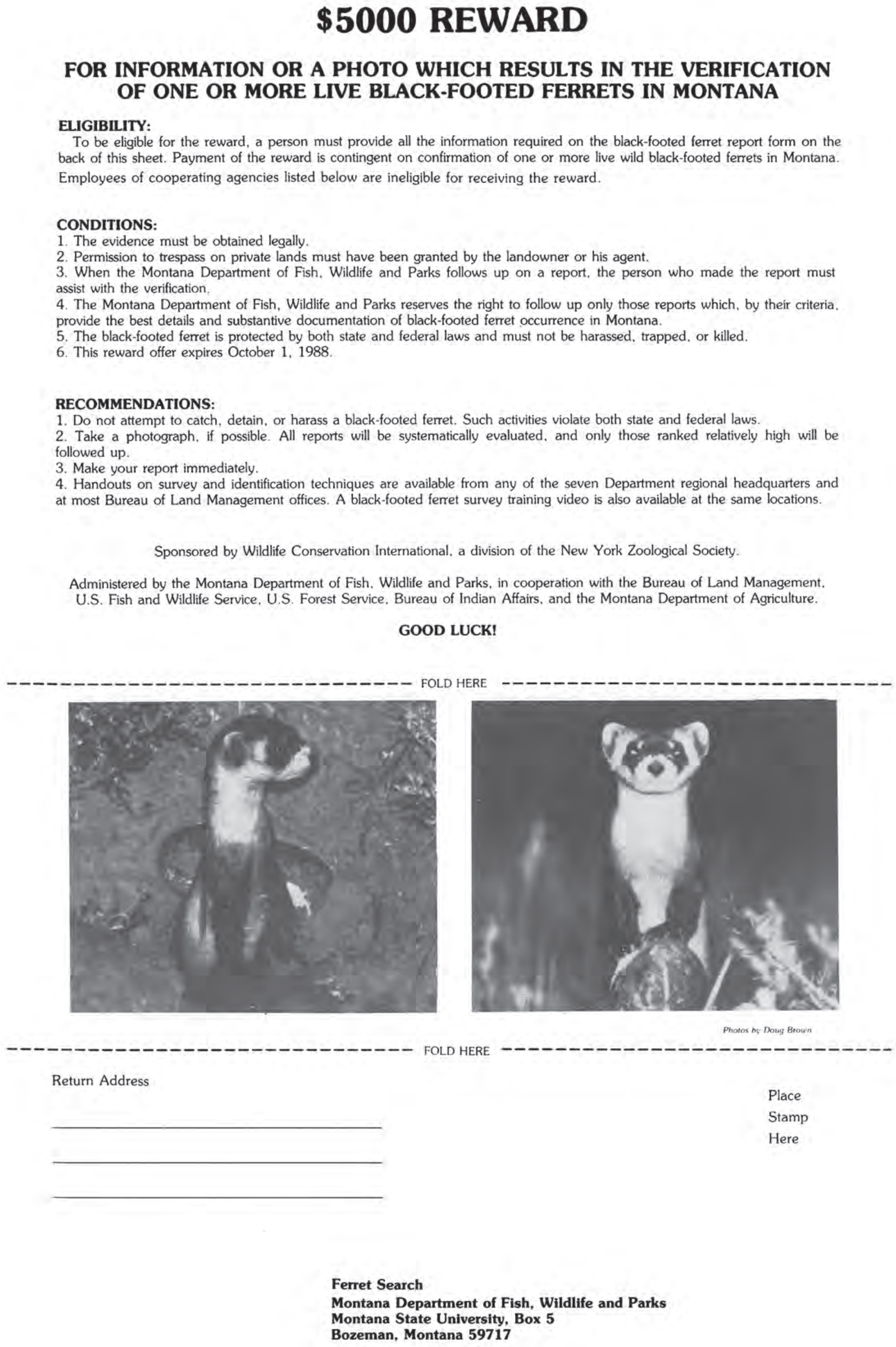
REWARD CONDITIONS: The ferret is an endangered species and is protected by very stringent federal and state laws. The reward WILL NOT be paid for any ferret caught in traps or killed by the finder. The reward will be given to the FIRST person providing information leading to the discovery and verification of the existence of black-footed ferrets (Mustela nigripes) in Wyoming. Skins and skeletons of ferrets struck accidently by cars and found along roads, reports of ferrets seen or photographs taken in an area where a representative of the "Ferret Search" project subsequently observes a ferret will qualify for the reward. A few ferrets have been seen in most parts of Wyoming in recent years. Ferrets eat prairie dogs and are usually found on or near prairie dog towns.

IDENTIFYING CHARACTERISTICS: The ferret is the size of a medium sized mink, about 18 inches long and 2.5 pounds. Unique features are black face mask and black feet. Do not confuse it with long-tailed weasels (no mask or black feet).

CONTACT: Tim W. Clark, Ferret Search, Box 1330, Jackson, Wyoming 83001; Telephone: 307-733-4806 as soon as possible after the sighting.

"Ferret Search" supported by National Geographic Society and The National Academy of Sciences. Reward offer expires 1 November, 1975.

Figure A2. A 1974 poster distributed by Tim Clark, offering a $50 reward for information leading to discovery of black-footed ferrets (*Mustela nigripes*).



$5000 REWARD

FOR INFORMATION OR A PHOTO WHICH RESULTS IN THE VERIFICATION OF ONE OR MORE LIVE BLACK-FOOTED FERRETS IN MONTANA

ELIGIBILITY:

To be eligible for the reward, a person must provide all the information required on the black-footed ferret report form on the back of this sheet. Payment of the reward is contingent on confirmation of one or more live wild black-footed ferrets in Montana. Employees of cooperating agencies listed below are ineligible for receiving the reward.

CONDITIONS:

1. The evidence must be obtained legally.
2. Permission to trespass on private lands must have been granted by the landowner or his agent.
3. When the Montana Department of Fish, Wildlife and Parks follows up on a report, the person who made the report must assist with the verification.
4. The Montana Department of Fish, Wildlife and Parks reserves the right to follow up only those reports which, by their criteria, provide the best details and substantive documentation of black-footed ferret occurrence in Montana.
5. The black-footed ferret is protected by both state and federal laws and must not be harassed, trapped, or killed.
6. This reward offer expires October 1, 1988.

RECOMMENDATIONS:

1. Do not attempt to catch, detain, or harass a black-footed ferret. Such activities violate both state and federal laws.
2. Take a photograph, if possible. All reports will be systematically evaluated, and only those ranked relatively high will be followed up.
3. Make your report immediately.
4. Handouts on survey and identification techniques are available from any of the seven Department regional headquarters and at most Bureau of Land Management offices. A black-footed ferret survey training video is also available at the same locations.

Sponsored by Wildlife Conservation International, a division of the New York Zoological Society.

Administered by the Montana Department of Fish, Wildlife and Parks, in cooperation with the Bureau of Land Management, U.S. Fish and Wildlife Service, U.S. Forest Service, Bureau of Indian Affairs, and the Montana Department of Agriculture.

GOOD LUCK!

FOLD HERE

Photos by Doug Brown

FOLD HERE

Return Address

____

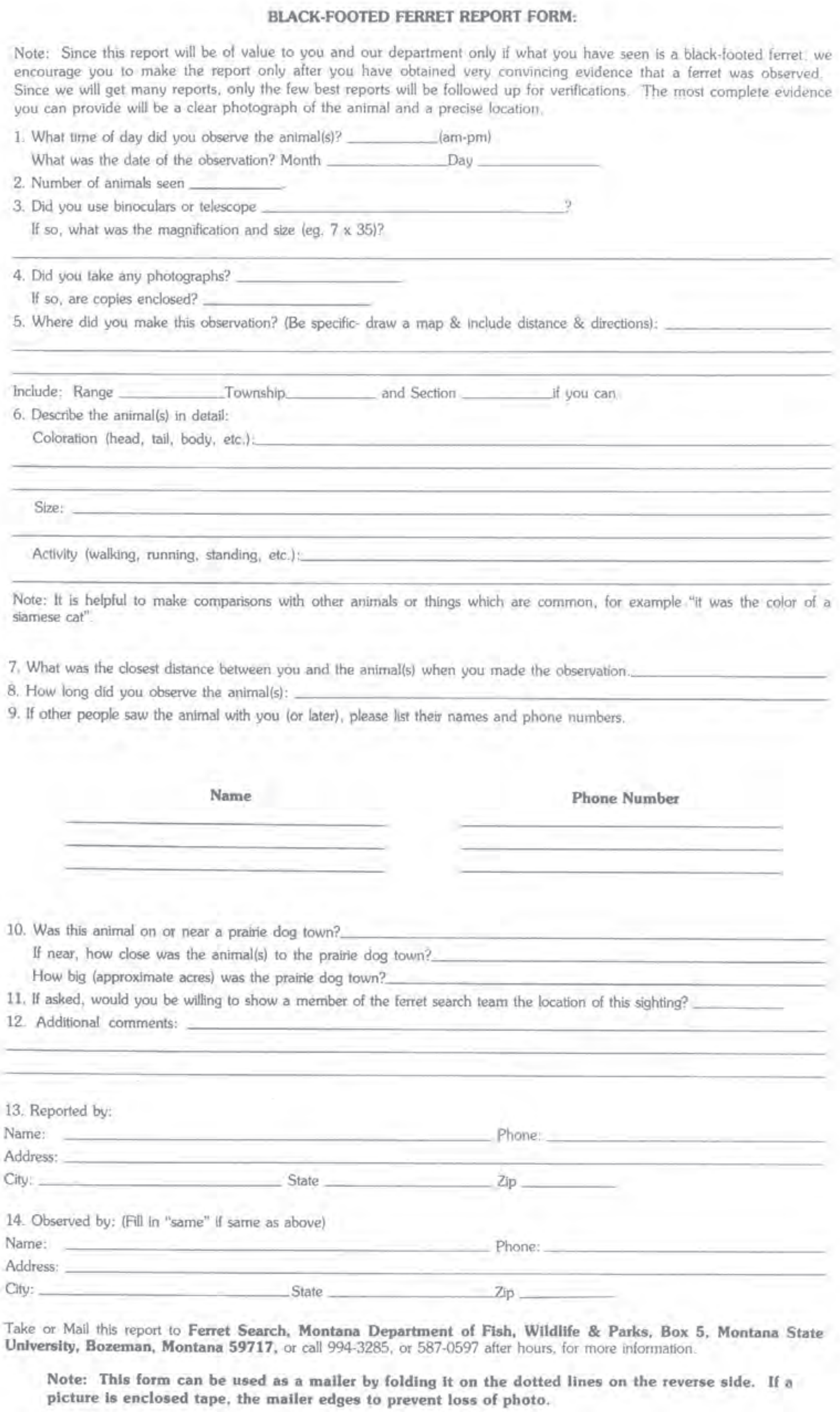
____

____

Place
Stamp
Here

Ferret Search
Montana Department of Fish, Wildlife and Parks
Montana State University, Box 5
Bozeman, Montana 59717

Figure A3. A pamphlet and report form, distributed in Montana starting in 1983, advertising a $5,000 reward for a verified black-footed ferret (*Mustela nigripes*) sighting.



BLACK-FOOTED FERRET REPORT FORM:

Note: Since this report will be of value to you and our department only if what you have seen is a black-footed ferret, we encourage you to make the report only after you have obtained very convincing evidence that a ferret was observed. Since we will get many reports, only the few best reports will be followed up for verifications. The most complete evidence you can provide will be a clear photograph of the animal and a precise location.

1. What time of day did you observe the animal(s)? ________(am-pm)
What was the date of the observation? Month ________Day ________
2. Number of animals seen ________.
3. Did you use binoculars or telescope ________?
If so, what was the magnification and size (eg. 7 x 35)?
____
4. Did you take any photographs? ________
If so, are copies enclosed? ________
5. Where did you make this observation? (Be specific- draw a map & include distance & directions): ________
____
____
Include: Range ________Township________ and Section ________if you can.
6. Describe the animal(s) in detail:
Coloration (head, tail, body, etc.):________
____
____
Size: ________
____
Activity (walking, running, standing, etc.):________
____

Note: It is helpful to make comparisons with other animals or things which are common, for example "it was the color of a siamese cat".

7. What was the closest distance between you and the animal(s) when you made the observation.________
8. How long did you observe the animal(s): ________
9. If other people saw the animal with you (or later), please list their names and phone numbers.

Name	**Phone Number**

10. Was this animal on or near a prairie dog town?________
If near, how close was the animal(s) to the prairie dog town?________
How big (approximate acres) was the prairie dog town?________
11. If asked, would you be willing to show a member of the ferret search team the location of this sighting? ________
12. Additional comments: ________
____
____

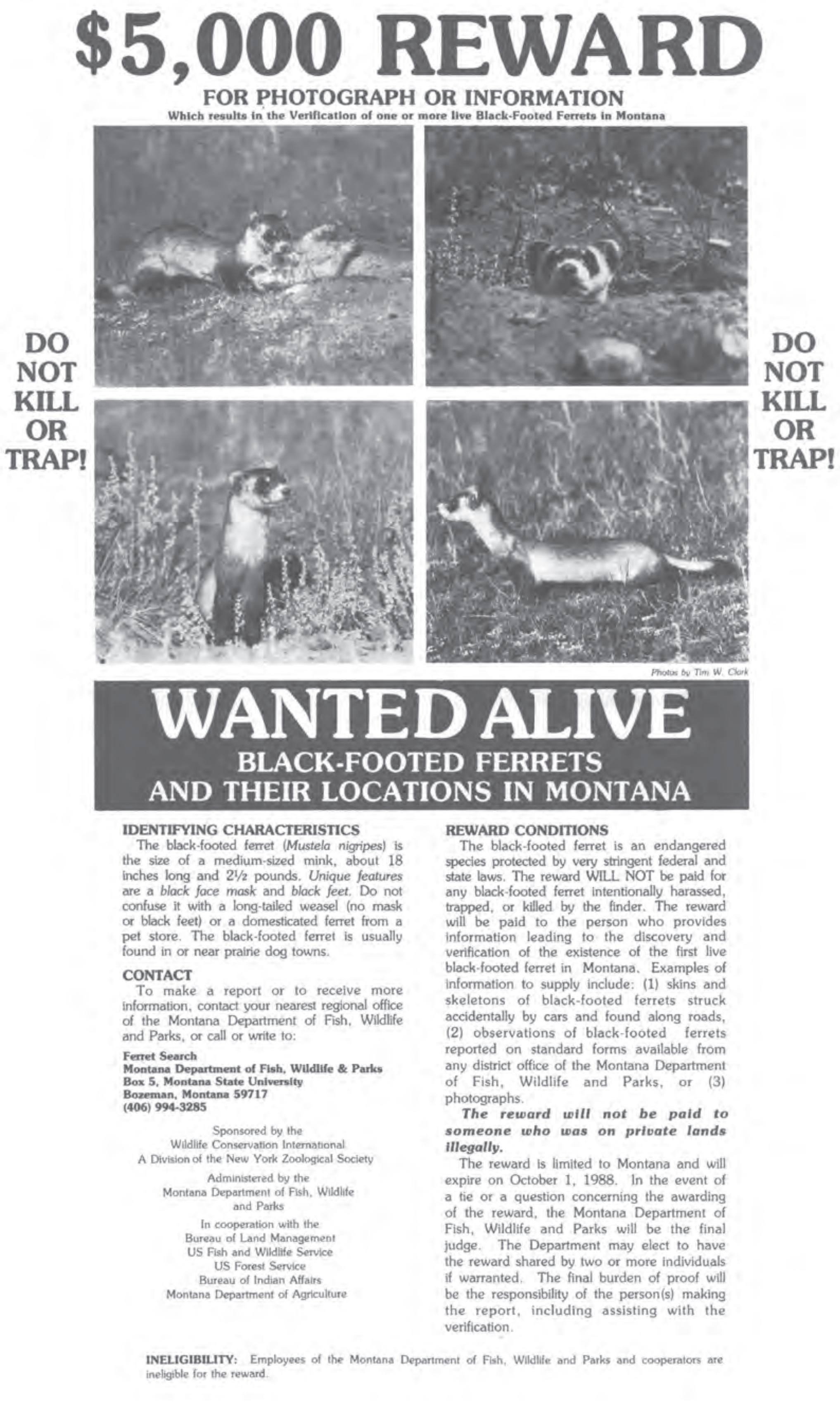
13. Reported by:
Name: ________ Phone: ________
Address: ________
City: ________ State ________ Zip ________

14. Observed by: (Fill in "same" if same as above)
Name: ________ Phone: ________
Address: ________
City: ________State ________Zip ________

Take or Mail this report to **Ferret Search, Montana Department of Fish, Wildlife & Parks, Box 5, Montana State University, Bozeman, Montana 59717,** or call 994-3285, or 587-0597 after hours, for more information.

Note: This form can be used as a mailer by folding it on the dotted lines on the reverse side. If a picture is enclosed tape, the mailer edges to prevent loss of photo.

Figure A3. A pamphlet and report form, distributed in Montana starting in 1983, advertising a $5,000 reward for a verified black-footed ferret (*Mustela nigripes*) sighting.—Concluded.



$5,000 REWARD

FOR PHOTOGRAPH OR INFORMATION

Which results in the Verification of one or more live Black-Footed Ferrets in Montana

DO NOT KILL OR TRAP!

DO NOT KILL OR TRAP!

Photos by Tim W. Clark

WANTED ALIVE

BLACK-FOOTED FERRETS AND THEIR LOCATIONS IN MONTANA

IDENTIFYING CHARACTERISTICS

The black-footed ferret (*Mustela nigripes*) is the size of a medium-sized mink, about 18 inches long and 2½ pounds. *Unique features* are a *black face mask* and *black feet*. Do not confuse it with a long-tailed weasel (no mask or black feet) or a domesticated ferret from a pet store. The black-footed ferret is usually found in or near prairie dog towns.

CONTACT

To make a report or to receive more information, contact your nearest regional office of the Montana Department of Fish, Wildlife and Parks, or call or write to:

Ferret Search
Montana Department of Fish, Wildlife & Parks
Box 5, Montana State University
Bozeman, Montana 59717
(406) 994-3285

Sponsored by the
Wildlife Conservation International
A Division of the New York Zoological Society

Administered by the
Montana Department of Fish, Wildlife
and Parks

In cooperation with the
Bureau of Land Management
US Fish and Wildlife Service
US Forest Service
Bureau of Indian Affairs
Montana Department of Agriculture

REWARD CONDITIONS

The black-footed ferret is an endangered species protected by very stringent federal and state laws. The reward WILL NOT be paid for any black-footed ferret intentionally harassed, trapped, or killed by the finder. The reward will be paid to the person who provides information leading to the discovery and verification of the existence of the first live black-footed ferret in Montana. Examples of information to supply include: (1) skins and skeletons of black-footed ferrets struck accidentally by cars and found along roads, (2) observations of black-footed ferrets reported on standard forms available from any district office of the Montana Department of Fish, Wildlife and Parks, or (3) photographs.

The reward will not be paid to someone who was on private lands illegally.

The reward is limited to Montana and will expire on October 1, 1988. In the event of a tie or a question concerning the awarding of the reward, the Montana Department of Fish, Wildlife and Parks will be the final judge. The Department may elect to have the reward shared by two or more individuals if warranted. The final burden of proof will be the responsibility of the person(s) making the report, including assisting with the verification.

INELIGIBILITY: Employees of the Montana Department of Fish, Wildlife and Parks and cooperators are ineligible for the reward.

Figure A4. A poster used to further advertise the Montana $5,000 reward supported by the New York Zoological Society, distributed in 1986–87.

$5,000 REWARD

FOR PHOTOGRAPH OR INFORMATION WHICH RESULTS IN VERIFICATION OF ONE OR MORE LIVE BLACK-FOOTED FERRETS

DO NOT KILL OR TRAP

Upper two black-footed ferrets by Dean Biggins. Ferret with prairie dog kill by Tim Clark. Ferret digging by Louise Forrest.

WANTED ALIVE

Black-footed ferrets and their locations

CHARACTERISTICS
The black-footed ferret *(Mustela nigripes)*, a nocturnal predator, is the size of a medium-sized mink, about 18 inches long and 2½ pounds. **Unique features are a black face mask and black legs.** Do not confuse it with a long-tailed weasel, a smaller animal without black legs. The domestic ferret sold in pet stores is not a black-footed ferret. The black-footed ferret is usually found in or near prairie dog towns.

DIGGINGS
Diggings can be evidence of ferret presence if they are found in winter and prairie dogs have been inactive. Black-footed ferret diggings are deposits of loose soil pulled from prairie dog size burrows (about 4-inches wide) and left on the surface of the ground or snow (see photograph). A digging should be reported if:

(1) it is deposited on snow and is accompanied by "twin print" type tracks (see illustration in margins)

OR

(2) it is deposited on the ground, is more than 3 feet long, is less than 12 inches wide, and has a trough or furrow-like depression centered along its length.

REWARD CONDITIONS
The black-footed ferret is an endangered species protected by very stringent federal and state laws. The reward WILL NOT be paid for any black-footed ferret intentionally harassed, trapped, or killed by the finder. The reward will be paid to the first person who provides information leading to the discovery and verification of the first live black-footed ferret in each state. Examples of information to supply include: (1) skins and skeletons of black-footed ferrets struck accidentally by cars and found along roads, (2) photographs of ferrets or ferret diggings, or (3) observations of black-footed ferrets or ferret diggings.

The reward will not be paid to someone who was on private lands illegally.

The reward offer is limited to participating states. In the event of a tie or a question concerning the awarding of the reward, the U.S. Fish and Wildlife Service will be the final judge. The Service may elect to have the reward shared by two or more individuals if warranted. The final burden of proof, including assisting with the verification, will be the responsibility of the person making the report. The reward offer is valid from September 1, 1987 through September 31, 1989.

CONTACT To make a report or to receive more information on how to find black-footed ferrets, call or write to:

Lou Hanebury - National Ecology Center, USFWS
1300 Blue Spruce Drive
Fort Collins, CO 80524
(303) 226-9460 Night (303) 224-2849

INELIGIBILITY Employees (and their relatives) of the U.S. Fish and Wildlife Service, State Conservation Agencies, and cooperators are ineligible for the reward.

Reward sponsored by the Wildlife Conservation International, a division of the New York Zoological Society.

Figure A5. The poster used to advertise the New York Zoological Society's $5,000 reward after the reward was offered nationally during 1987–89.

$10,000 REWARD

FOR PHOTOGRAPH OR INFORMATION WHICH RESULTS IN VERIFICATION OF ONE OR MORE LIVE BLACK-FOOTED FERRETS

DO
NOT
KILL
OR
TRAP

Upper two black-footed ferrets by Dean Biggins. Ferret with prairie dog kill by Tim Clark. Ferret digging by Louise Forrest.

WANTED ALIVE

Black-footed ferrets and their locations

CHARACTERISTICS

The black-footed ferret *(Mustela nigripes)*, a nocturnal predator, is the size of a medium-sized mink, about 18 inches long and 2½ pounds. **Unique features are a black face mask and black legs.** Do not confuse it with a long-tailed weasel, a smaller animal without black legs. The domestic ferret sold in pet stores is not a black-footed ferret. The black-footed ferret is usually found in or near prairie dog towns.

DIGGINGS

Diggings can be evidence of ferret presence if they are found in winter and prairie dogs have been inactive. Black-footed ferret diggings are deposits of loose soil pulled from prairie dog size burrows (about 4-inches wide) and left on the surface of the ground or snow (see photograph). A digging should be reported if:

(1) it is deposited on snow and is accompanied by "twin print" type tracks (see illustration in margins)

OR

(2) it is deposited on the ground, is more than 3 feet long, is less than 12 inches wide, and has a trough or furrow-like depression centered along its length.

REWARD CONDITIONS

The black-footed ferret is an endangered species protected by very stringent federal and state laws. The reward WILL NOT be paid for any black-footed ferret intentionally harassed, trapped, or killed by the finder. The reward will be paid to the first person who provides information leading to the discovery and verification of the first live black-footed ferret in each state. Examples of information to supply include: (1) skins and skeletons of black-footed ferrets struck accidentally by cars and found along roads, (2) photographs of ferrets or ferret diggings, or (3) observations of black-footed ferrets or ferret diggings.

The reward will not be paid to someone who was on private lands illegally.

The reward offer is limited to participating states. In the event of a tie or a question concerning the awarding of the reward, the U.S. Fish and Wildlife Service will be the final judge. The Service may elect to have the reward shared by two or more individuals if warranted. The final burden of proof, including assisting with the verification, will be the responsibility of the person making the report. The reward offer is valid from September 1, 1987 through December 31, 1990.

CONTACT To make a report or to receive more information on how to find black-footed ferrets, call or write to:

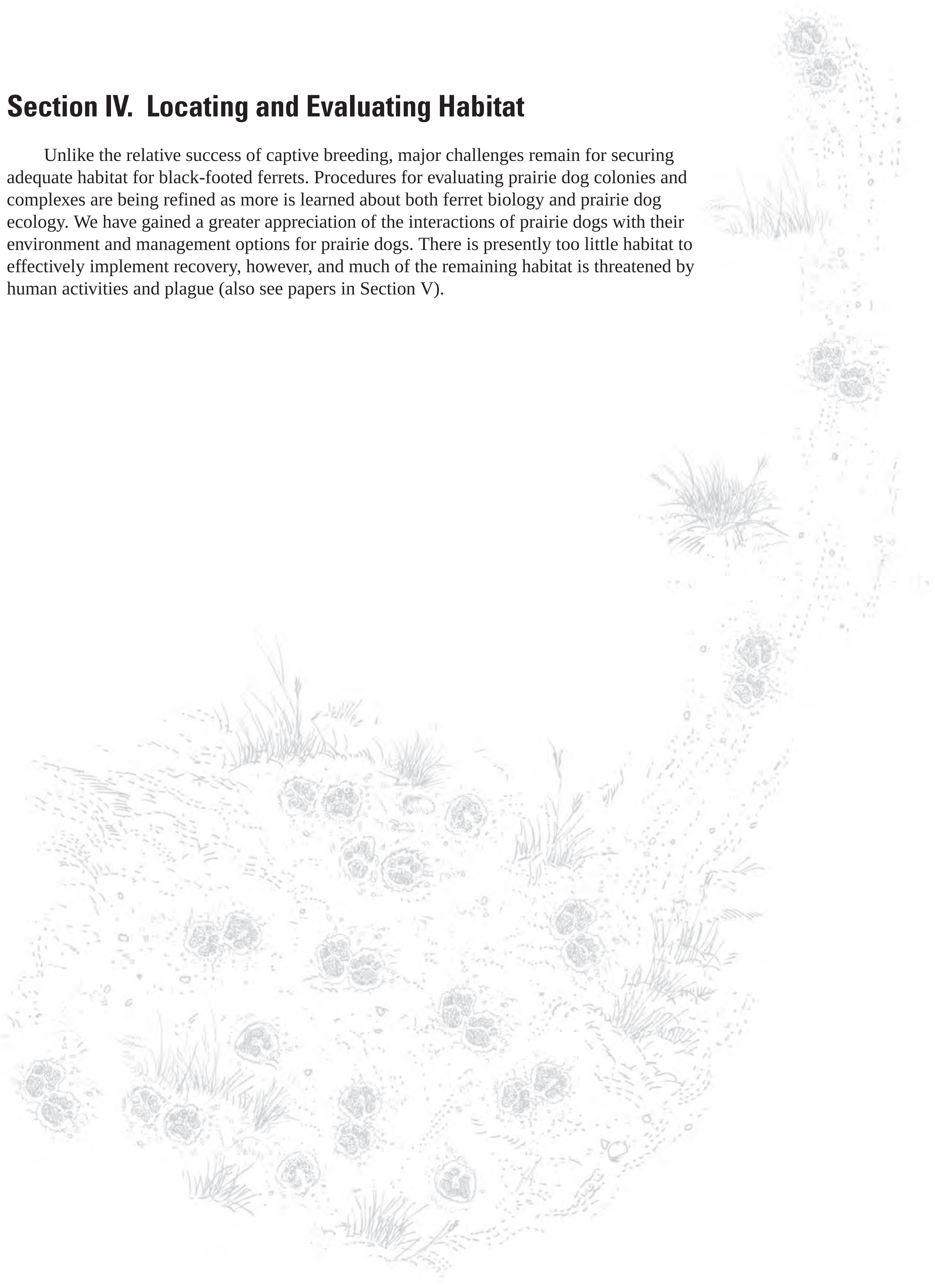
INELIGIBILITY Employees (and their relatives) of the U.S. Fish and Wildlife Service, State Conservation Agencies, and cooperators are ineligible for the reward.

Reward sponsored by the Wildlife Conservation International, a division of the New York Zoological Society.

Figure A6. The poster used to advertise the New York Zoological Society's national reward of $10,000 offered in 1989.

Section IV. Locating and Evaluating Habitat

Unlike the relative success of captive breeding, major challenges remain for securing adequate habitat for black-footed ferrets. Procedures for evaluating prairie dog colonies and complexes are being refined as more is learned about both ferret biology and prairie dog ecology. We have gained a greater appreciation of the interactions of prairie dogs with their environment and management options for prairie dogs. There is presently too little habitat to effectively implement recovery, however, and much of the remaining habitat is threatened by human activities and plague (also see papers in Section V).



Areas Where Habitat Characteristics Could Be Evaluated To Identify Potential Black-footed Ferret Reintroduction Sites and Develop Conservation Partnerships

By Robert J. Luce[1]

Abstract

This paper is an attempt to develop a new, broad list of potential black-footed ferret (*Mustela nigripes*) reintroduction sites across its historical range. I reviewed reports and publications that identified active, inactive, and potential reintroduction sites, including unpublished reports generated by State wildlife agencies and universities. I contacted local experts and reviewed the published and unpublished literature describing colony locations of three species of prairie dogs (*Cynomys* spp.). I list active reintroduction sites and others already planned and identify 70 other sites in the historical range of the black-footed ferret that might meet the biological and habitat suitability requirements for reintroduction of the species within 3–10 years, contingent upon directed management emphasis, State and Federal agency management priority, and, if on private land, landowner concurrence through agreements or incentives. I present this conceptual effort in the hope that identification of sites at this level will prompt discussion, revisions, additions, and deletions and will result in the formation of conservation partnerships that will contribute to black-footed ferret recovery.

Keywords: black-footed ferret, conservation, *Cynomys*, endangered species, *Mustela nigripes*, prairie dog, reintroduction

Introduction

Although many known, large prairie dog (*Cynomys* spp.) complexes have previously been identified, I believe that this paper is the first serious attempt to develop a new, broader list of potential reintroduction sites across the historical range of the black-footed ferret (*Mustela nigripes*). Some of these sites have been considered before, but many have not, or at least not in the same context as in the current effort. I present this conceptual effort in the hope that identification of the sites at this level will prompt discussion, revisions, additions, and deletions, and result in the formation of conservation partnerships that will contribute to black-footed ferret recovery.

Past efforts to identify sites have been constrained by the need to immediately take into account land ownership, plague history, and other factors that do not constrain the current conceptual effort. I hope that this paper prompts many who have not considered contributing to black-footed ferret recovery to get involved with a site in their locality. Several States that have not been involved in black-footed ferret recovery in the past have not previously participated in site identification.

I recognize that there are issues other than ecological ones that must be addressed when identifying potential reintroduction sites; however, I believe that recovery of the black-footed ferret depends first and foremost upon identifying and conserving areas that meet or have the potential to meet the biological parameters for establishment and long-term survival of viable populations. I believe that social and economic issues, including private land rights, economic concerns related to forage competition between livestock and prairie dogs, and others, are vitally important. I also believe, however, that a start must be made. Changes in Federal land management priorities, cooperative management planning on Federal lands, and financial incentives or regulatory assurances for private landowners or tribal governments must logically follow after habitat suitability has been established.

Recovery efforts for the endangered black-footed ferret have faced numerous and significant challenges, including extirpation of the species in the wild, development of captive breeding techniques and reintroduction methods, lack of adequate financial resources, and organizational inefficiencies (Forrest and others, 1985; Clark, 1986; U.S. Fish and Wildlife Service, 1988; Miller and others, 1996). Much work has been accomplished, and much remains to be done in these areas and others, but at present I believe that the most fundamental obstacle to meaningful recovery of the black-footed ferret in the wild is the availability of suitable habitat, both in quantity and quality; that is, prairie dog colonies of sufficient size and proximity to other colonies (Chaplin and others, 1996; Lomolino and others, 2002; Luce, 2003). There is a critical need to identify suitable sites and begin management of those sites for reintroduction and recovery. In fact, this may be the ultimate challenge to black-footed ferret recovery because it involves the greatest potential conflict with other land-use interests. Political and social barriers often surpass in difficulty those in the biological arena.

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[1] P.O. Box 7, Sierra Vista, AZ 85636.

In the late 1980s, spurred by the need to utilize animals produced by captive breeding, biologists identified several potential reintroduction sites. In 1988–89, R. Luce (written commun., 1995) developed a list of 18 potential reintroduction sites in Wyoming by using data from a variety of sources. Conway (1989) evaluated six of those sites and concluded that only two had prairie dog numbers suitable for black-footed ferret reintroduction. Closer examination of other sites in Wyoming, as well as sites in Arizona, Colorado, South Dakota, and Utah, revealed that many were more or less unsuitable at the time of evaluation for various reasons, principally because prairie dogs did not occupy the sites to the extent that earlier evaluations had recorded or assumed (M. Lockhart, written commun., 1999–2003). Ranking of sites suitable for black-footed ferret reintroduction and recovery has emphasized the importance of large complexes of prairie dog colonies and identification of multiple sites. Additionally, it has been assumed that more densely occupied black-tailed prairie dog (*C. ludovicianus*) colonies are preferable to less dense white-tailed (*C. leucurus*) or Gunnison's (*C. gunnisoni*) prairie dog colonies and that a plague-free environment is preferable. New data documenting maintenance and/or growth of both prairie dog and black-footed ferret populations at reintroduction sites on Gunnison's and white-tailed prairie dog complexes where plague is present in Arizona (B. Van Pelt, oral commun., 2004) and Wyoming (M. Grenier, oral commun., 2004) indicate that these assumptions warrant further investigation.

A revision of the current Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) is underway, so it is important to note that I do not intend to supersede the site selection process that will be a part of the revised plan. The revised plan may include new downlisting and delisting goals for number of black-footed ferrets and number or location of reintroduction sites, but in either case a large number of potential reintroduction sites must be identified. I offer a new baseline list that includes contributions from all portions of the species' historical range, both previously overlooked sites and recently identified sites. I do not attempt to identify long-term black-footed ferret recovery needs for various areas of the species range because a rangewide delisting goal has not been identified and because a related method for apportioning recovery responsibilities among political jurisdictions has not been formalized to date (see Ernst and others, this volume).

The most promising recovery sites already have active reintroduction programs in place. I believe that several new sites with potential for adequate occupied habitat to be present within 3–10 years should be identified for each of the political jurisdictions within the historical range of the black-footed ferret. It is not appropriate to wait for a definitive answer as to the number of black-footed ferrets necessary for delisting or the amount of actual habitat that will be needed. Many more sites must be evaluated than are currently being considered because environmental unknowns, especially plague and drought, affect the viability of individual sites; therefore, longevity cannot be predicted or guaranteed. In addition, political and social attitudes may change, resulting in loss of support for maintaining adequate occupied prairie dog habitat at a given site. I identify a large number of sites so that no one site will be under pressure for rapid development, but yet the presence of the sites on the list will allow agencies to begin planning toward management of those sites, potentially allowing a significant number of them to be available for black-footed ferret reintroduction in 3–10 years.

Methods

I reviewed previous efforts that identified active, inactive, and potential black-footed ferret reintroduction sites, including the U.S. Fish and Wildlife Service (FWS) reintroduction site list (Conway, 1989; M. Lockhart, written commun., 1999–2003; fig. 1). I also reviewed published literature, including Lair and Mecham (1991), Vanderhoof and Robel (1994), Ernst (2001), and Johnson and others (2003). In addition, I reviewed available information regarding other potential sites, including unpublished reports generated by State wildlife agencies

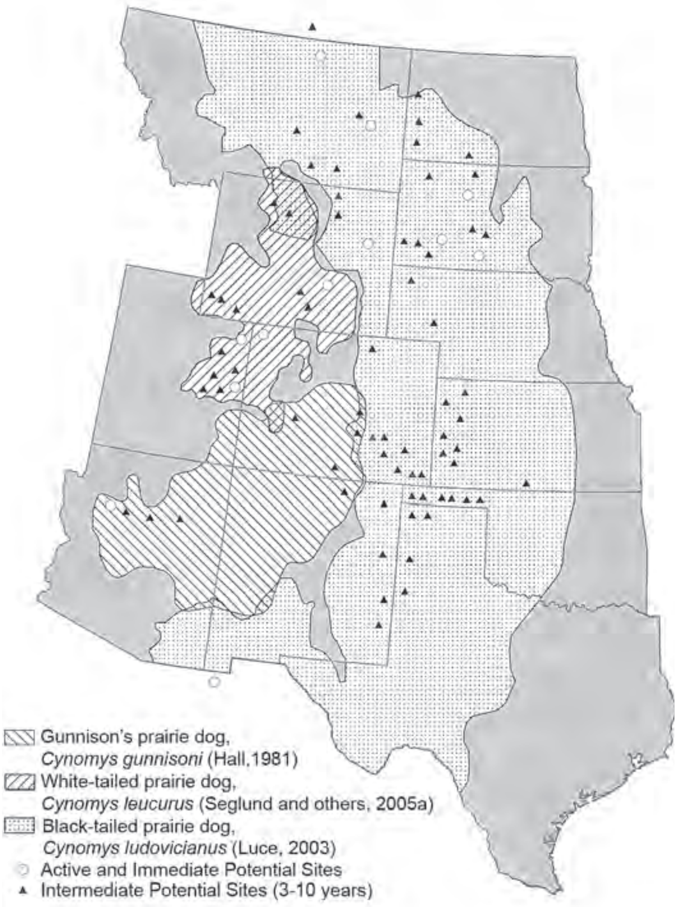

Figure 1. Location of eight active black-footed ferret (*Mustela nigripes*) reintroduction sites (1990–2004); three Immediate Potential Sites (1–3 years); and 70 Intermediate Potential Sites, at which, pending further evaluation, opportunities for reintroducing ferrets may exist in 3–10 years.

and universities, and contacted local experts. I had personal communication with Steve Whiteman, Southern Ute Tribe; Craig Knowles, FaunaWest Wildlife Consultants; Derrick Holdstock and Heather Whitlaw, Texas Parks and Wildlife Department; Julianne Hoagland, Oklahoma Department of Wildlife Conservation; Pamela Schnurr, Colorado Division of Wildlife; Dave Wagner, Northern Arizona University; Bill Woodson, U.S. Army; Mike Albee, U.S. Bureau of Land Management; Tim Byer and Dave Augustine, U.S. Forest Service; Joe Truett, Turner Endangered Species Fund; Allison Puchniak, Montana Department of Fish, Wildlife and Parks; Terry Enk, New Mexico Department of Game and Fish; Pete Gober, Randy Matchett, Scott Larson, John Nysted, and Lou Hanebury, U.S. Fish and Wildlife Service; Mark Lomolino, State University of New York, College of Environmental Science and Forestry; Amy Seglund and Craig McLaughlin, Utah Division of Wildlife Resources; Pat Fargey, Grasslands National Park, Canada; Martin Grenier, Wyoming Game and Fish Department; Tim Vosburgh, Intertribal Black-tailed Prairie Dog Coordinator; Bill Van Pelt, Arizona Game and Fish Department; Rurik List, Instituto de Ecologia, Ciudad Universitaria Coyoacan, Mexico; Travis Livieri, Prairie Wildlife Research; Mike Fritz, Nebraska Game and Parks Commission; and Sandy Hagen, North Dakota Game and Fish Department.

Information was acquired for 12 States within the historical range of the black-footed ferret, five Native American reservations, two States in Mexico, and one Canadian Province. The foundation for this effort was provided by intensive and extensive inventories and preparation of management plans for black-tailed prairie dogs, as summarized in Luce (2003); white-tailed prairie dog survey data, as summarized in Seglund and others (2005a); and Gunnison's prairie dog survey data, as summarized in Seglund and others (2005b).

I use the following terminology. Active Sites are those at which black-footed ferrets have been previously released and are being actively managed. Immediate Potential Sites are those already identified by the Black-footed Ferret Recovery Implementation Team and upon which reintroduction work has begun. Intermediate Potential Sites are those at which opportunities may exist in the 3- to 10-year time frame.

Planning efforts conducted by recovery partners require a queue of potential sites. I provide a locally specific list of all potential black-footed ferret reintroduction sites across the species' historical range but focus on Intermediate Potential Sites since these provide the next step in black-footed ferret reintroduction beyond management of Active Sites. Reintroduction efforts could begin at an Intermediate Potential Site before the minimum occupied habitat identified was available if expansion could be reasonably anticipated within a decade. Therefore, sites that are now below the minimum threshold for occupied habitat are also listed in this paper, anticipating that they have potential to meet or exceed the minimum within 10 years. Although I surmise that long-term potential sites may exist, I do not list those here.

At existing black-footed ferret reintroduction sites, as well as in State black-tailed prairie dog management plans, contiguous habitat is defined as a complex of colonies in which no colony is farther than 7 km from another colony (Biggins and others, 1993). A colony is defined as a concentration of black-tailed prairie dogs with an average density of at least 4.05 individuals/ha (Luce, 2003) or as a concentration of white-tailed prairie dogs with a minimum of 20 burrow openings/ha on 5-ha parcels (Biggins and others, 1993; Seglund and others, 2005a). Colony has not yet been defined for Gunnison's prairie dogs, but the species is biologically similar to the white-tailed prairie dog. Although this rigorous definition was not used to identify the Intermediate Potential Sites in this paper, it must be assumed that sites will be required to meet a similar standard eventually before their full potential for maintenance of a long-term, viable black-footed ferret population can be achieved.

Based on bioenergetic (Biggins and others, 1993) and behavioral considerations (R. Matchett and T. Livieri, oral commun., 2003) and known densities of the respective species, I began with the premise that the minimum adult population of 30 individuals identified in the 1988 recovery plan (U.S. Fish and Wildlife Service, 1988) might require 1,215 ha of contiguous, occupied black-tailed prairie dog habitat; 1,823 ha of contiguous, occupied Gunnison's prairie dog habitat; or 2,430 ha of contiguous, occupied white-tailed prairie dog habitat. I recognize that prairie dog densities vary between sites and at individual sites on an annual basis, but I found it necessary to use averages in this evaluation process.

I also worked from the premise that the amount of extant, occupied habitat noted above may not be necessary to identify potential reintroduction sites and perhaps begin black-footed ferret releases. I suggest that 607.5 ha of contiguous, occupied black-tailed prairie dog habitat; 911.3 ha of contiguous, occupied Gunnison's prairie dog habitat, or 1,215.0 ha of contiguous, occupied white-tailed prairie dog habitat may be sufficient to begin management planning or possible experimental release of black-footed ferrets. The choice of 50 percent was arbitrary and assumes that prairie dog colonies will grow. Of course, many other factors may affect suitability of a reintroduction site, but I believe that these rough measures may allow preliminary identification of a queue of sites that can be further evaluated.

I characterized sites in regard to the species of prairie dog present, the amount of occupied prairie dog habitat, and disease status in a manner similar to that used by M. Lockhart (written commun., 1999–2003). Many of these sites have been recently identified as a result of ongoing inventories of prairie dog habitat.

Results

Current and potential black-footed ferret reintroduction sites are listed below for U.S. States and some Native American tribal lands, Canadian Provinces, and Mexican States having historical prairie dog habitat. Each is preceded by background information related to prairie dog populations. Many sites are in the early stages of identification and mapping; some may not yet be fully mapped, and some have no data on the amount of occupied prairie dog habitat or density of prairie dogs. Sites are summarized in table 1 (Active and Immediate Potential Sites) and table 2 (Intermediate Potential Sites), and locations are illustrated in figure 1.

Arizona

Black-tailed and Gunnison's prairie dogs occurred in Arizona historically. The black-tailed prairie dog was extirpated from Arizona in the 1930s; therefore, reintroduction of black-tailed prairie dogs would be necessary before their colonies could serve as reintroduction sites for black-footed ferrets. In 2002, Wagner and Drickamer (2002) collected data from all potential sources and identified 400 locations with Gunnison's prairie dog colonies. They revisited 293 colonies in 2000 and 2001 and found that 270 were active. Gunnison's prairie dogs are located in northern Arizona from the Colorado River to Flagstaff and eastward along the Little Colorado River. No survey data are available for the Navajo Indian Reservation, which may comprise as much as one-third of the potential range.

Active Sites

Aubrey Valley

Arizona has one active black-footed ferret reintroduction site on a Gunnison's prairie dog complex in Aubrey Valley (Coconino, Yavapai, and Mojave Counties) in the northwestern part of the State (fig. 1). Reintroduction efforts began in 1996. The site is designated a black-footed ferret nonessential experimental population, and releases of captive black-footed ferrets are ongoing. Approximately 25 black-footed ferrets occur in the wild there at present. Total occupied prairie dog habitat is approximately 12,039 ha on a mixture of private, State, and Hualapai Indian Reservation lands. Monitoring at this site has not documented plague during the last 20 years, although it has been noted in the region. Prairie dog populations can be severely affected by drought at this site (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

East of Seligman

Approximately 2,502 ha of active Gunnison's prairie dog colonies were present on-site in 1992. The site is a large open grassland bisected by I-40. Occupied habitat was reduced considerably in 1996 because of a plague epizootic, but recovery began in 2001. This area is <10 km from Aubrey Valley (Wagner and Drickamer, 2002; D. Wagner, oral commun., 2003).

West of Dilkon, Navajo Indian Reservation

The Navajo Natural Heritage Program surveyed Gunnison's prairie dogs in this area to investigate its potential as a black-footed ferret reintroduction site. The survey documented approximately 3,200 ha of occupied habitat. This area was affected by plague in 1996, and there has been little recovery to date (Wagner and Drickamer, 2002; D. Wagner, oral commun., 2003).

Table 1. Sites at which black-footed ferrets (*Mustela nigripes*) have been reintroduced and are being managed (Active Sites), and sites identified by the Black-footed Ferret Recovery Implementation Team where some work preparatory to reintroduction has been done (Immediate Potential Sites).

State	Site name	Nearest town	Plague status
Active Sites			
Arizona	Aubrey Valley	Seligman	Not present
Colorado	Colorado/Utah	Dinosaur	Present
Montana	North-central Phillips County	Malta	Present
South Dakota	Cheyenne River Indian Reservation		
	Conata Basin/Badlands National Park	Wall	Not present
	Rosebud Indian Reservation	Winner	Not present
Utah	Colorado/Utah	Dinosaur, Colo.	Present
Wyoming	Shirley Basin	Medicine Bow	Present
Chihuahua, Mexico	Janos	Janos	Not present
Immediate Potential Sites			
Montana	Custer Creek	Miles City	Unknown
Utah	Cisco Desert	Green River	Present
Wyoming	Thunder Basin National Grassland	Bill	Present

Table 2. Sites at which, pending further evaluation, opportunities for reintroducing black-footed ferrets (*Mustela nigripes*) may exist in 3–10 years (Intermediate Potential Sites; *n* = 70).

State or Province	Site name	Nearest town	Plague status
Arizona	East of Seligman	Seligman	Present
	West of Dilkon, Navajo Indian Reservation	Dilkon	Present
	West of Wupatki National Monument	Flagstaff	Present
Colorado	Pueblo County	Pueblo	Present
	Weld County	Greeley	Present
	Bent County	Lamar	Present
	Baca County	Springfield	Present
	Crowley County	Rocky Ford	Present
	Pueblo Army Depot	Pueblo	Present
	Fort Carson	Colorado Springs	Present
	Comanche National Grassland, Carrizo Unit	Pritchett	Present
	Comanche National Grassland, Timpas Unit, and Pinon Canyon Maneuver Site	La Junta	Present
	Cimarron National Grassland	Springfield	Present
	BLM Twin Lakes Allotment	Alamosa	Present
	Parlin	Gunnison	Present
Kansas	Z-Bar Ranch	Medicine Lodge	Plague free
	Logan County	Colby	Plague free
	Northern Kearny County	Garden City	Plague free
	Greeley County	Horace	Plague free
	Rawlins County	Atwood	Plague free
	Hamilton County	Syracuse	Plague free
	Southern Kearny County	Garden City	Plague free
	Sherman County	Colby	Plague free
Montana	Leachman complex	Billings	Present
	Northern Cheyenne Indian Reservation	Colstrip	Present
	Miles City BLM District	Miles City	Present
	Fort Benton-Roundup-Harlowton area	Roundup	Present
Nebraska	Blue Creek Ranch	Oshkosh	Plague free
	Oglala National Grassland	Chadron	Plague free
New Mexico	Vermejo Park Ranch	Raton	Unknown
	Quay/Curry County interface	Tucumcari	Unknown
	Roosevelt County/Grulla National Wildlife Refuge	Portales	Unknown
	Lea County	Lovington	Unknown
	Union County	Clayton	Unknown
North Dakota	Horse Creek area, Little Missouri National Grassland	Williston	Unknown
	Standing Rock Indian Reservation	North Lemmon	Unknown
	South Unit, Theodore Roosevelt National Park	Dickinson	Plague free
	Little Missouri River	Bowman	Plague free

Table 2. Sites at which, pending further evaluation, opportunities for reintroducing black-footed ferrets (*Mustela nigripes*) may exist in 3–10 years (Intermediate Potential Sites; *n* = 70)—Concluded.

State or province	Site name	Nearest town	Plague status
Oklahoma	Southwest Cimarron County	Boise City	Plague free
	Texas County No. 1	Guymon	Plague free
	Texas County No. 2	Guymon	Plague free
	Beaver County No. 1	Beaver	Plague free
	Beaver County No. 2	Beaver	Plague free
South Dakota	Pine Ridge Indian Reservation	Pine Ridge	Plague free
	Standing Rock Indian Reservation	Lemmon	Plague free
	Lower Brule Indian Reservation	Pierre	Plague free
	Wind Cave National Park	Hot Springs	Plague free
	Grand River National Grassland	Lodgepole	Plague free
	Bad River Ranches	Pierre	Plague free
	Smithwick area, Buffalo Gap National Grassland	Hot Springs	Plague free
Texas	Rita Blanca National Grassland	Dalhart	Unknown
	Muleshoe National Wildlife Refuge	Lubbock	Present
	Sherman County	Dumas	Unknown
	Deaf Smith County	Amarillo	Unknown
Utah	Buckhorn and Crescent Junction	Price	Present
	Twelvemile Flat	Green River	Present
	Eightmile Flat (Myton Bench)	Green River	Present
	Sunshine Bench/Brush Creek	Green River	Present
	Buckhorn Flat	Price	Present
Wyoming	Meeteetse	Meeteetse	Present
	Bolton Ranch	Saratoga	Present
	Carter	Kemmerer	Present
	Cumberland	Kemmerer	Present
	Fifteenmile	Worland	Present
	Flaming Gorge	Green River	Present
	Shamrock Hills	Rawlins	Present
	Kaycee	Kaycee	Unknown
	Sheridan Local Training Center	Sheridan	Unknown
Saskatchewan, Canada	Grasslands National Park	Swift Current	Unknown

West of Wupatki National Monument

Gunnison's prairie dogs are present at this site north of Flagstaff. A complex of 950 ha was mapped in 2001. Plague has occurred, but the extent has not been quantified (Wagner and Drickamer, 2002; D. Wagner, oral commun., 2003).

Colorado

Black-tailed prairie dogs, white-tailed prairie dogs, and Gunnison's prairie dogs occur in Colorado. Complete location data are not available for Gunnison's prairie dogs since some potential habitat in southwestern Colorado has not been surveyed. White-tailed prairie dogs are also currently being surveyed in northwestern Colorado. Black-tailed prairie dogs occur in all counties in the historical range in the eastern one-third of the State, and recent surveys indicate 255,596 ha of occupied habitat (Colorado Division of Wildlife, 2003). Location data from that survey are not available to the author at this time, however. EDAW, Inc. (2000) identified the 10 counties with the largest amount of active, occupied habitat in the State: Pueblo (8,989 ha), Weld (8,146 ha), Bent (6,914 ha), Baca (5,816 ha), Crowley (5,475 ha), Adams (5,372 ha), Prowers (5,161 ha), Boulder (4,668 ha), Cheyenne (3,717 ha), and Kiowa (3,629 ha). EDAW, Inc. (2000) identified 17 colonies >405 ha and 45 colonies from 203 to 405 ha in the black-tailed prairie dog range in Colorado.

Active Sites

Colorado/Utah

White-tailed prairie dogs occupy the only active black-footed ferret reintroduction site in Colorado. The site is located in northwestern Colorado in Moffat and Rio Blanco Counties and extends into Utah (Uintah County) and Wyoming (Sweetwater County). The Wyoming portion of the site, called Kinney Rim, has virtually no active colonies at the current time. Reintroduction efforts began in 1998. The site is designated a black-footed ferret nonessential, experimental population, and releases of captive black-footed ferrets are ongoing. A small population of black-footed ferrets occurs in the wild there at present. Total occupied prairie dog habitat is approximately 20,250 ha, primarily on U.S. Bureau of Land Management (BLM) land, and plague is present. Potential habitat present in the Colorado portion of this site is estimated at 45,553 ha (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

Pueblo County

Black-tailed prairie dogs occupy this site. The northern half of the county, north of the City of Pueblo, has the largest concentration of colonies and the majority of the 8,989 ha of colonies identified in the county (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Weld County

Black-tailed prairie dogs occupy this site. The northeastern half of the county, northeast of the City of Greeley, has the largest concentration of colonies and the majority of the 8,146 ha of colonies identified in the county (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Bent County

Large black-tailed prairie dog colonies occur in the northern and western parts of the county, encompassing the majority of the 6,914 ha identified (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Baca County

The western one-half of the county, centered on the town of Pritchett, has the largest concentration of black-tailed prairie dog colonies and has the majority of the 5,816 ha identified in the county (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Crowley County

Large black-tailed prairie dog colonies occur in several places in the county, encompassing 5,475 ha (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Pueblo Army Depot

Black-tailed prairie dogs occupy this site, which is on a U.S. Army installation. Approximately 1,066 ha of occupied habitat were present before a plague outbreak in 2003. The site is managed by the military and is protected from shooting and poisoning except where black-tailed prairie dogs may constitute a human health hazard (B. Woodson, oral commun., 2003). A large area of occupied habitat also occurs on private lands adjacent to Pueblo Army Depot in El Paso County (EDAW, Inc., 2000).

Fort Carson

Black-tailed prairie dogs occupy this site, which is on a U.S. Army installation. Approximately 1,418 ha of occupied habitat were present before a plague outbreak occurred in 2002 or 2003. The site is managed by the military and is protected from shooting and poisoning except where black-tailed prairie dogs may constitute a human health hazard (B. Woodson, oral commun., 2003). A large area of occupied habitat also occurs on private lands adjacent to Fort Carson, particularly along the southern boundary in Pueblo County (EDAW, Inc., 2000).

Comanche National Grassland, Carrizo Unit

Recent GIS analyses identified 46,395 ha of potential black-tailed prairie dog habitat on this site in Baca County. Potential habitat was defined as land with clay or loamy soil and <5 percent slope. Of this potential habitat, 1,622 ha are currently occupied, with an additional 450 ha occupied outside of potential habitat (primarily on lands mapped as sandy soils, most likely because of inaccurate generalities in the soil map). The Carrizo Unit has extremely fragmented land ownership. Intermingled private lands have even higher densities of colonies (due to higher grazing intensity), but landowners have strongly negative attitudes toward black-tailed prairie dogs. Approximately 2,076 ha of occupied black-tailed prairie dog habitat occurs on National Forest lands, and the amount of occupied habitat on intermingled private lands is unknown (D. Augustine, written commun., 2003).

Comanche National Grassland, Timpas Unit, and Pinon Canyon Maneuver Site

Black-tailed prairie dogs occupy this site, which is on the Timpas Unit and the adjoining U.S. Army Pinon Canyon Maneuver Site. Together these areas provide a large block of land in public ownership with little fragmentation. The Timpas Unit includes a number of private inholdings but is far less fragmented than the Carrizo Unit (above). The amount of occupied habitat in the Timpas Unit is lower than in the past because of plague. A total of 35,917 ha of potential habitat exists, of which 192 ha are currently occupied. An additional 41 ha are outside the area mapped as suitable habitat, for a total of 233 ha on the Timpas Unit. Occupied habitat on the Pinon Canyon Maneuver Site totaled 143 ha when last mapped (D. Augustine, written commun., 2003).

Cimarron National Grassland

Black-tailed prairie dogs occupy this site, which has approximately 16,200 ha of potential habitat, 1,296 ha of which were occupied in 2003. The area is bounded on the north by cropland and on the south by riparian/sand sagebrush (*Artemisia filifolia*) habitat. The Cimarron is separated from the Comanche by sand sagebrush habitat unsuitable for black-tailed prairie dog expansion (D. Augustine, written commun., 2003).

Bureau of Land Management Twin Lakes Allotment

Gunnison's prairie dogs occur at this site on public land in Conejos County, approximately 32 km south of Alamosa. The area supports a large complex of colonies dating back to the 1970s, many of which are old or inactive. Existing occupied habitat is approximately 512 ha (M. Albee, oral commun., 2003).

Parlin

Gunnison's prairie dogs occur at this site, which is on public land 19 km southeast of Gunnison in Gunnison County. The amount of occupied habitat in 1980 was 497 ha (M. Albee, oral commun., 2003).

Kansas

Only black-tailed prairie dogs occur in Kansas. Recent surveys estimate 52,861 ha of occupied habitat in western Kansas (Kansas Black-tailed Prairie Dog Working Group, 2002). The estimate of suitable habitat in Kansas based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 60,181 ha.

Intermediate Sites

Z-Bar Ranch

Black-tailed prairie dogs occupy this site, which is on property owned by Turner Enterprises, Inc., approximately 40 km southwest of Medicine Lodge in Barber County. The site currently supports 101 ha of occupied habitat and is growing steadily. Grassland conservation and black-tailed prairie dog expansion are high priority management objectives (J. Truett, oral commun., 2003).

Logan County

This county contained the largest complex (3,522 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Northern Kearny County

The northern part of this county contained the second largest complex (1,104 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Greeley County

This county contained the third largest complex (826 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Rawlins County

This county contained the fourth largest complex (448 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Hamilton County

This county contained the fifth largest complex (423 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Southern Kearny County

The southern part of this county contained the sixth largest complex (400 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Sherman County

This county had the highest number of colonies and highest occupied area in the 1990–92 survey: 60 colonies and 1,420 ha (Vanderhoof and Robel, 1992, 1994). It also had significant occupied black-tailed prairie dog habitat in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Montana

Both black-tailed and white-tailed prairie dogs occur in Montana. White-tailed prairie dogs are confined to a very small area near the border with Wyoming and occupy roughly 40 ha of habitat at the present time; therefore, no black-footed ferret reintroduction potential exists for the foreseeable future. Black-tailed prairie dogs occur in the eastern part of the State, and the best estimate of occupied area is 36,450 ha (Montana Prairie Dog Working Group, 2002). The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 97,349 ha.

Active Sites

North-central Phillips County

Black-tailed prairie dogs occupy this site. Black-footed ferret releases have occurred since 1994. Occupied prairie dog habitat was 12,014 ha in the mid-1990s, with 5,457 ha occurring on Fort Belknap Indian Reservation, 4,472 ha on BLM lands, and 2,085 ha on Charles M. Russell National Wildlife Refuge. The area was heavily affected by plague in the late 1990s. The black-footed ferret population is very low at the current time. Land ownership is mixed private, Federal, and tribal (M. Lockhart, written commun., 1999–2003).

Immediate Potential Sites

Custer Creek

Black-tailed prairie dogs occupy this site in Prairie and Custer Counties, which contains >100 colonies and 1,705 ha of occupied habitat on a mixture of State, private, and BLM lands. Plague has not been documented since 1996. Since this site is in an area of checkerboard land status, private interests control the site potential (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

The following locations were identified in the Conservation Plan for Black-tailed and White-tailed Prairie Dogs in Montana (Montana Prairie Dog Working Group, 2002) as 4 of the 10 largest known prairie dog complexes in Montana in 2000.

Leachman Complex

This site is entirely on tribal land in the northwest portion of the Crow Indian Reservation in Yellowstone and Big Horn Counties, and once supported an estimated 4,050–4,860 ha of occupied prairie dog habitat (L. Hanebury, oral commun., 2003). The site included >2,835 ha of occupied prairie dog habitat in recent times but suffered a plague outbreak prior to 2003. Approximately 2,430 ha remained in two colonies in the southwest and central portions of the area in 2003. With translocations, this complex could be viable within a few years (L. Hanebury, oral commun., 2003). Since surveys of suitable habitat on the Crow Indian Reservation have not been completed, sites other than the Leachman site may also exist (L. Hanebury, oral commun., 2003).

Northern Cheyenne Indian Reservation

Suitable habitat exists on the Reservation along the upper Tongue River in Big Horn and Rosebud Counties as well as on adjacent U.S. Forest Service and private lands. Occupied habitat exceeded 5,265 ha prior to a recent plague outbreak. With the help of translocations, this site grew to approximately 2,025 ha in 2003 (L. Hanebury, oral commun., 2003).

Miles City Bureau of Land Management District

Potential habitat exists in Custer and Prairie Counties. This site is mixed private and BLM lands and supported approximately 2,430 ha of prairie dogs in 2000; however, recent plague outbreaks have reduced the size of this complex to approximately 1,337 ha. A change in land ownership resulted in reduced access for mapping, which may have exaggerated the apparent decline in occupied habitat (L. Hanebury, oral commun., 2003).

Fort Benton-Roundup-Harlowton Area

Suitable habitat exists along the upper Musselshell River in Yellowstone, Stillwater, Musselshell, Golden Valley, Wheatland, and Petroleum Counties. The area is mixed private, BLM, and FWS lands and supported >2,430 ha of prairie dogs in 2000 (L. Hanebury, oral commun., 2003).

Nebraska

Only black-tailed prairie dogs occur in Nebraska. Recent surveys estimate 32,400 ha of occupied habitat (M. Fritz, oral commun., 2003) in western Nebraska. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 55,588 ha.

Intermediate Potential Sites

Blue Creek Ranch

This site, which is owned by Turner Enterprises, Inc., is 16 km northeast of Oshkosh and currently has 8 ha of occupied habitat, which is expanding. Grassland conservation and black-tailed prairie dog expansion are high management priorities (J. Truett, oral commun., 2003).

Oglala National Grassland

This site is located in Sioux and Dawes Counties and currently has 284 ha of occupied black-tailed prairie dog habitat. The Oglala National Grassland will require time to expand existing prairie dog habitat and to consolidate the land base to improve the management potential (S. Larson, written commun., 2003).

New Mexico

Black-tailed and Gunnison's prairie dogs occur in New Mexico. Recent black-tailed prairie dog surveys estimate 24,300 ha of occupied habitat (Johnson and others, 2003) in eastern New Mexico. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 35,288 ha. Surveys are ongoing for Gunnison's prairie dog, but there is no estimate of current occupied habitat.

Intermediate Potential Sites

Vermejo Park Ranch

This site, which is owned by Turner Enterprises, Inc., is located 40 km southwest of Raton and currently has 689 ha of occupied habitat, which is expanding rapidly. Grassland conservation and black-tailed prairie dog expansion are high priorities (J. Truett, oral commun., 2003).

Quay/Curry County Interface

This site is south of Tucumcari and contains >3,848 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 19 ha, and the maximum area of a single colony is 152 ha (Johnson and others, 2003).

Roosevelt County/Grulla National Wildlife Refuge

This site is south of Portales and contains >5,265 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 35 ha, and the maximum size of a single colony is 339 ha (Johnson and others, 2003).

Lea County

This site is northeast of Lovington and contains approximately 9,720 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 60 ha, and the maximum area of a single colony is 956 ha (Johnson and others, 2003). Plague has recently been active in this area, but impacts have not been quantified (P. Gober, oral commun., 2003).

Union County

This site is southwest of Clayton and contains approximately 3,240 ha of occupied habitat. The mean size of colonies is 41 ha, and the maximum area of a single colony is 292 ha (Johnson and others, 2003).

North Dakota

Only black-tailed prairie dogs occur in North Dakota. Recent surveys estimate 8,303 ha of occupied habitat (Knowles, 2003) in western North Dakota. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 40,723 ha.

Intermediate Potential Sites

Horse Creek Area, Little Missouri National Grassland

Black-tailed prairie dogs occupy 162 ha at this site in McKenzie County in western North Dakota. The site has strong potential to reach biological readiness for black-footed ferret reintroduction within 10 years, but local support cannot be predicted at this time. The site is included in the most recent land management plans for Little Missouri National Grassland and is plague free (S. Larson, written commun., 2003).

Standing Rock Indian Reservation

Black-tailed prairie dogs occupy 1,215 ha at this site in Sioux County. Colonies are scattered over a large area, and the land base is a checkerboard of private and tribal lands. The area is plague free (S. Larson, written commun., 2003).

South Unit, Theodore Roosevelt National Park

Black-tailed prairie dogs occupy 729 ha at this site in Billings County. In 2002, 61 active colonies were mapped (Knowles, 2003). Knowles (2003) predicted that the site potential on the national park is >2,633 occupied ha based on the amount of suitable habitat present. Additional suitable habitat occurs on adjacent private land, and the area is plague free (Knowles, 2003).

Little Missouri River

Black-tailed prairie dogs occupy this site in Slope County. The site had 345 ha of occupied habitat in 2002. Significant biological potential exists if private land issues can be addressed. The area is plague free (Knowles, 2003).

Oklahoma

Only black-tailed prairie dogs occur in Oklahoma. Recent surveys estimate 26,007 ha of occupied habitat (J. Hoagland, oral commun., 2003) in western Oklahoma. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 27,806 ha.

Intermediate Potential Sites

Sites in Oklahoma have previously been described as clusters of colonies (M. Lomolino, written commun., 2003).

Cimarron County

This site is in the southwestern corner of the county. Cluster A had 12 colonies totaling 345 ha, and Cluster B had 6 colonies with a total of 652 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Texas County No. 1

This site is in the north-central part of the county. Cluster C had 12 colonies with a total of 332 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Texas County No. 2

This site is in the east-central part of the county. Cluster D had 18 colonies with a total of 302 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Beaver County No. 1

This site is in the east-central part of the county. Cluster E had 10 colonies with a total of 93 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Beaver County No. 2

This site is in the south-central part of the county. Cluster F had 34 colonies with a total of 319 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

South Dakota

Only black-tailed prairie dogs occur in South Dakota. A 2001 survey estimated 64,800 ha of occupied habitat (South Dakota Prairie Dog Work Group, 2001) in western South Dakota. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 80,786 ha.

Active Sites

Cheyenne River Indian Reservation

Black-tailed prairie dogs occupy this site in Dewey and Ziebach Counties. Total occupied habitat is 17,861 ha in three separate complexes, one of which is 8,424 ha. An operational prairie management program is currently pursuing black-footed ferret reintroduction. There is no history of plague in the area (M. Lockhart, written commun., 1999–2003).

Conata Basin/Badlands National Park

Black-tailed prairie dogs occupy this site in Pennington, Shannon, and Jackson Counties. Total occupied habitat is 6,116 ha, with 4,779 ha on U.S. Forest Service lands and 1,337 ha on National Park Service lands. The estimated potential for the area based on suitable habitat is 7,128 ha. There is no history of plague in the area (M. Lockhart, written commun., 1999–2003).

Rosebud Indian Reservation

Black-tailed prairie dogs occupy 28,350 ha at this site in Todd and Mellette Counties, 18,225 ha of which is on tribal trust lands. There is no history of plague in the area (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

Pine Ridge Indian Reservation

Black-tailed prairie dogs occupy 20,250–40,500 ha on tribal lands at this site in Shannon County. The site has the biological capacity to support a large black-footed ferret population but may be constrained by social, cultural, and political factors (S. Larson, written commun., 2003).

Standing Rock Indian Reservation

Black-tailed prairie dogs occupy 2,835 ha at this site in Corson County. Black-tailed prairie dogs are scattered over a large area, and the land base is a mixture of private and tribal. There is no history of plague in the area (S. Larson, written commun., 2003).

Lower Brule Indian Reservation

Black-tailed prairie dogs occupy 11,745 ha at this site in Stanley and Lyman Counties. There is no history of plague in the area (S. Larson, written commun., 2003).

Wind Cave National Park

Black-tailed prairie dogs occupy 689 ha at this site in Custer County. Biologically, this site could be ready for black-footed ferret reintroduction within a few years, and the National Park Service is supportive. There is no history of plague in the area (S. Larson, written commun., 2003).

Grand River National Grassland

Black-tailed prairie dogs occupy 648 ha at this site in Perkins and Corson Counties. Biologically, this site is not ready for black-footed ferret reintroduction, as it needs time for black-tailed prairie dogs to expand occupied habitat. The U.S. Forest Service needs to consolidate its land base; however, it has identified the site for prairie dog expansion in the most recent land management plan. There is no history of plague in the area (S. Larson, written commun., 2003).

Bad River Ranches

Black-tailed prairie dogs occupy this site on lands owned by Turner Enterprises, Inc., in Stanley and Jones Counties, 16 km southwest of Pierre. The site currently has 506 ha of occupied habitat and is growing steadily. Grassland conservation and black-tailed prairie dog expansion are high priorities. There is no history of plague in the area (J. Truett, oral commun., 2003).

Smithwick Area, Buffalo Gap National Grassland, Fall River Ranger District

Black-tailed prairie dogs occupy 405 ha at this site in Custer County. From a biological standpoint, the site could be ready for black-footed ferret reintroduction within 5 years. The site was included in the most recent land management plan for Buffalo Gap National Grassland. There is no history of plague in the area (S. Larson, written commun., 2003).

Texas

Only black-tailed prairie dogs occur in Texas. Ongoing surveys currently estimate 79,785 ha of occupied habitat in western Texas (D. Holdstock, oral commun., 2003). The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 118,717 ha.

Intermediate Potential Sites

Rita Blanca National Grassland

Black-tailed prairie dogs occupy this site north of Dalhart in Dallam County. The site was identified by Lair and Mecham (1991) as having >4,050 ha of occupied habitat, with 49 colonies >41 ha in size and >1.0 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Muleshoe National Wildlife Refuge

Black-tailed prairie dogs occupy this site northwest of Lubbock in Bailey County. It was identified by Lair and Mecham (1991) as having >2,835 ha of occupied habitat, with 25 colonies >41 ha in size and >1.0 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Sherman County

Black-tailed prairie dogs occupy this site north of Dumas. It was identified by Lair and Mecham (1991) as having >3,240 ha of occupied habitat, with 32 colonies >41 ha in size and 1.5 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Deaf Smith County

Black-tailed prairie dogs occupy this site southwest of Amarillo. It was identified in Lair and Mecham (1991) as having >5,670 ha of occupied habitat, with 55 colonies >41 ha in size and 1.5 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Utah

Gunnison's prairie dogs and white-tailed prairie dogs occur in Utah. Data on locations and occupied area are still being developed for both species.

Active Sites

There is one active black-footed ferret reintroduction site in Utah (see discussion under Colorado).

Immediate Potential Sites

Cisco Desert

White-tailed prairie dogs occur at this potential site identified by the Black-footed Ferret Recovery Program. The site was mapped in 1986 (Boschen, 1986) and again in 2002 (Seglund and others, 2005a). The site is on public land in Grand County in east-central Utah along I-70 from east of Green River to the Colorado border. Land ownership is mixed private, State, and Federal (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

Buckhorn and Crescent Junction

White-tailed prairie dogs occupy this site in Emery and Grand Counties in south-central Utah. According to C. McLaughlin (oral commun., 2003), Cedar Creek Associates mapped 7,644 ha, including both active and inactive colonies, in this complex on public lands in 1985. The area mapped extended south of Huntington to I-70 along State Highway 10, east to State Highway 6, and along I-70 to Thompson Springs. In 2002, mapping within the same area recorded 7,881 ha, including active and inactive colonies, approximately a 3 percent increase from 1985 (C. McLaughlin, written commun., 2003).

Twelvemile Flat

White-tailed prairie dogs occur at this site on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. Twelvemile Flat contained 363 ha of occupied habitat in 1985. The site was resurveyed in 1992–93 (Cranney and Day, 1994) and found to have 771 ha of occupied habitat, slightly over double the amount present in 1985. In 2002, mapping located 365 ha of occupied habitat (C. McLaughlin, written commun., 2003).

Eightmile Flat (Myton Bench)

White-tailed prairie dogs occur at this site on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. Eightmile Flat contained 2,673 ha of occupied habitat in 1985. The site was resurveyed in 1999 and found to have increased by 9 percent, to 2,936 ha of occupied habitat (C. McLaughlin, written commun., 2003).

Sunshine Bench/Brush Creek

White-tailed prairie dogs occur at these sites on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. The sites were mapped to evaluate their suitability for black-footed ferret reintroduction in 1992–93 (Cranney and Day, 1994). The Sunshine Bench complex contained 2,085 ha of occupied habitat in 1992–93, while the adjacent Brush Creek area contained 145 ha of occupied habitat. The combined occupied area of Sunshine Bench and Brush Creek was 7,837 ha in 2002 (C. McLaughlin, written commun., 2003).

Buckhorn Flat

White-tailed prairie dogs occur at this site on public lands 56 km south of Price. The estimated occupied habitat at the site is 2,412 ha (A. Seglund, written commun., 2003).

Wyoming

Black-tailed and white-tailed prairie dogs occur in Wyoming. Black-tailed prairie dogs occur in the eastern one-third of the State. Recent occupied habitat estimates range widely, but the current estimate is 50,625 ha (M. Grenier, written commun., 2003). The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 64,059 ha. White-tailed prairie dogs occur in the west-central part of the State, and surveys are underway to estimate occupied habitat.

Active Sites

Shirley Basin

Shirley Basin/Medicine Bow is the only active black-footed ferret reintroduction site in Wyoming and occurs in the white-tailed prairie dog range. The site was fully mapped in 1989 (Conway, 1989) and again in 1990 by using a combination of aerial transects and ground verification (Hnilicka and Luce, 1992). In 1990, intensive mapping showed the complex to contain 59,726 ha (Parrish and Luce, 1990). Captive-bred black-footed ferrets were released from 1991 to 1994, and the highest number of black-footed ferrets found on subsequent surveys was in 2004, when 85 individuals were located during spotlight surveys (Grenier and others, 2004) of less than 20 percent of the occupied habitat (based on 1990 mapping data). Therefore, considerable potential exists for a large, contiguous population of black-footed ferrets or several subpopulations. It is important to note that both prairie dogs and black-footed ferrets have persisted with plague present since at least 1987 (Orabona-Cerovski, 1991).

Immediate Potential Sites

Thunder Basin National Grassland

Black-tailed prairie dogs occur at this site in Campbell, Converse, and Weston Counties. The site is identified as a black-footed ferret reintroduction site in the current Forest Plan for the Medicine Bow National Forest/Thunder Basin National Grassland. There was no history of plague before 2001 when an extensive die-off occurred, reducing occupied habitat by over 4,050 ha. Recovery is occurring. Prior to the plague outbreak, occupied black-tailed prairie dog habitat was 8,079 ha, including 7,290 ha on U.S. Forest Service land and 789 ha on State land. The U.S. Forest Service estimates that there are 193,590 ha of potential habitat on its lands in this area of Wyoming (T. Byer, written commun., 2003).

Intermediate Potential Sites

Meeteetse

White-tailed prairie dogs occupy this site west of Meeteetse in Park County. This site, from which all of the black-footed ferret captive breeding stock was taken, had 4,930 ha of occupied habitat in 1982, just after black-footed ferrets were first discovered, and a high population of 129 black-footed ferrets (43 adults, 25 litters) in 1984. Because of plague in white-tailed prairie dogs, occupied habitat was reduced to roughly 2,029 ha by 1989, 2 years after all extant black-footed ferrets were captured for captive breeding (Black-footed Ferret Advisory Team, 1990). The site has not shown significant recovery of prairie dogs since 1989 (Biggins, 2003). The habitat capability of the site remains, including old burrow systems, so the potential exists for recovery to sufficient occupied habitat for black-footed ferret reintroduction within 10 years.

Bolton Ranch

White-tailed prairie dogs occupy this site west of Saratoga in Carbon County. Land ownership is a checkerboard of public and private lands. The site had 4,500 ha of occupied habitat in 1989 when it was first surveyed (Conway, 1989). No surveys have been conducted since then (Grenier and others, 2003; R. Luce, written commun., 1995).

Carter

White-tailed prairie dogs occupy this site 32 km southeast of Kemmerer, on BLM lands in Lincoln County. The site has not been fully mapped or surveyed to determine prairie dog density. It contained more than 4,050 ha of occupied habitat when partially mapped in the 1980s (Grenier and others, 2003; R. Luce, written commun., 1995). The Carter site is potentially connected to another site (Moxa) which is 32 km north of Kemmerer, indicating that an extremely large complex may exist in this area. Moxa was identified in the mid-1990s when 17,415 ha of occupied habitat were mapped, and the site has not been resurveyed (Grenier and others, 2003; B. Luce, unpub. data, 1995).

Cumberland

White-tailed prairie dogs occupy this site southwest of Kemmerer in Lincoln County. Land ownership is a checkerboard of public and private lands. The site was fully mapped and preliminary density data were collected in the 1980s (Clark and Campbell, 1981). Occupied habitat was 4,293 ha. The site has not been remapped.

Fifteenmile

White-tailed prairie dogs occupy this site on BLM land 40 km west of Worland in Hot Springs County. The site contained 3,078 ha of occupied habitat when mapped in the 1980s and has not been remapped (Grenier and others, 2003; R. Luce, written commun., 1995).

Flaming Gorge

White-tailed prairie dogs occupy this site on BLM land 64 km south of Green River in Sweetwater County. The site was intensively mapped in 1989 and contained 3,049 ha of occupied habitat (Martin and Luce, 1990). It has not been remapped.

Shamrock Hills

White-tailed prairie dogs occupy this site on BLM land 16 km north of Rawlins in Carbon County. The site was mapped in the 1980s and had >4,050 ha of occupied habitat. The site has not been remapped (Grenier and others, 2003; R. Luce, written commun., 1995).

Kaycee

Black-tailed prairie dogs occupy this site west of the town of Kaycee in Johnson County, primarily on private land. This site was discovered recently and has not been mapped, but it is estimated that >1,215 ha of occupied habitat are present (R. Luce, unpub. data, 2003).

Sheridan Local Training Center

Black-tailed prairie dogs occupy this site on a U.S. Army installation adjacent to Sheridan in Sheridan County. The site contained 284 ha of occupied habitat in 2001, and adjacent private and State lands had a substantial amount of additional occupied habitat (R. Luce, unpub. data, 2003).

Canada

Only black-tailed prairie dogs occur in Canada, which is the northern extent of the range of the species.

Intermediate Potential Sites

Grasslands National Park and Vicinity

Black-tailed prairie dogs occur at this site in Saskatchewan, 160 km south of Swift Current. The site has 25 colonies containing a minimum of 1,044 ha. It has been partially mapped since 1993 but was fully mapped for comparative purposes from 1998 to 2002 and had a stable occupied area for that time period (P. Fargey, written commun., 2003).

Mexico

Black-tailed prairie dogs occur in northern Mexico, the southern extent of the range, and are the only species of prairie dog in Mexico in the historical range of the black-footed ferret.

Active Sites

Janos

Black-tailed prairie dogs occur at this site north of Nuevo Casas Grandes in Chihuahua. Estimated occupied prairie dog habitat is 19,845 ha, and the potential suitable habitat is 55,080 ha. Land ownership is divided between Federal Ejidos and private ownership. This is a large prairie dog complex and may have the potential for one contiguous black-footed ferret population or several subpopulations. No management plan exists for the area (R. List, oral commun., 2003).

Intermediate Potential Sites

There are no Intermediate Potential Sites in Mexico.

Discussion

It is clear from past efforts that a “best and only” methodology for successful black-footed ferret reintroduction has not been unequivocally established. The 1988 recovery plan (U.S. Fish and Wildlife Service, 1988) encourages experimentation. It also emphasizes a management philosophy important for both establishing and maintaining reintroduced populations whereby the broadest possible distribution of black-footed ferrets might be achieved. This risk management approach is important to protect the species overall from adverse impacts that may occur locally, especially disease.

Preparation of this paper does not constitute a proposed State or Federal action at any of the proposed sites; it is merely a conceptual approach to aid in black-footed ferret recovery. Many steps will be required before any site can eventually receive ferrets; however, I do not believe that it is necessary or appropriate to wait for final biological, social, and political issues to be addressed at a given site in order for it to be considered for the list of potential reintroduction sites. This conceptual exercise identifies sites based entirely on either a minimum area of occupied prairie dog habitat or a small but increasing prairie dog population at a site that has the habitat characteristics necessary to support black-footed ferrets. I recognize that myriad actions would be necessary before black-footed ferrets could actually be released at a given site, especially where private lands are involved.

The general limitation of lack of habitat or habitat availability is shared with many other species. But in the case of the black-footed ferret, which is a highly specialized prey/habitat obligate of prairie dogs, dependence has proven to be especially catastrophic because of the dramatic reduction of its prey over the past century by adverse land-use practices such as prairie conversion to cropland, poisoning to reduce forage competition with domestic livestock, and sylvatic plague, an exotic disease catastrophic to prairie dogs (Cain and others, 1972; Hansen, 1988; Cully, 1993; Van Pelt, 1999; U.S. Fish and Wildlife Service, 2000; Cully and Williams, 2001; Antolin and others, 2002; Luce, 2003). Despite these potential conflicts and future challenges, identification of appropriate sites for black-footed ferret reintroduction has been ongoing for over two decades.

Although occupied prairie dog habitat has been significantly reduced since western settlement (Hoogland, 1995; Miller and Cully, 2001), it has been only in the last decade that the degree of both the quantity and quality of this loss relative to potential black-footed ferret recovery has been recognized. At present there may not be sufficient occupied prairie dog habitat in total in the historical ranges of the black-tailed prairie dog, white-tailed prairie dog, and Gunnison’s prairie dog, either in quantity or quality, for the black-footed ferret to be fully recovered, especially if black-footed ferret populations are to be broadly represented geographically as a precaution against depressant stochastic influences (M. Lockhart, written commun., 1999–2003).

The 1988 Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) set a downlisting goal for the species at 1,500 adults in 10 or more populations dispersed across its historical range, with no single population being less than 30 adults. Downlisting the species would move it from endangered to threatened status but would not represent complete recovery. Delisting the black-footed ferret through recovery sufficient to obviate its endangered status and permit its removal from the endangered species list (pursuant to the Endangered Species Act of 1973, as amended) would require even more recovery sites.

I suggest that it may be necessary to evaluate an order of magnitude more sites to achieve complete recovery and delisting, or 100 sites across the historical range of the species. These sites should be widely dispersed and represent the variety of habitats available, including different prairie dog species, ecological circumstances, disease prevalence, and the like. Since some sites may prove not to be usable for biological, social, or other reasons, or may not be successful, it will be necessary to consider many.

Plague is a confounding factor. Annual monitoring to document plague activity and the amount of habitat affected would assist prairie dog and black-footed ferret management. Continuing research on the mechanisms by which plague is spread, pretreatment of prairie dogs, and posttreatment of burrows to kill fleas and thus reduce the magnitude of an epizootic may allow practical management of the disease in the next 10 years. Meanwhile, maintaining spatial distribution of prairie dog complexes and isolated colonies over the entire range to act as reservoirs to replace prairie dogs lost to plague, as well as development of black-footed ferret reintroduction sites east of the plague line (in the plague-free area), will greatly assist in managing the impacts of the disease on prairie dogs.

In my opinion, data presented by Cully and Williams (2001) suggest that a fundamental change may be occurring in prairie dog ecology whereby some large colonies, especially those of black-tailed prairie dogs, may not persist when repeatedly challenged by plague. Persistence of only small colonies or complexes may have serious implications for black-footed ferret recovery. Extensive habitat will be necessary for reintroduction success, especially in the absence of management, and few large sites may persist at their full habitat capability in the face of repeated plague epizootics. On the other hand, recent surveys of white-tailed prairie dogs and black-footed ferrets in Shirley Basin, Wyo., indicate that these areas may have proportionately higher value than previously thought because both prairie dogs and black-footed ferrets have maintained significant populations in the presence of plague since monitoring was begun in 1991 (Luce, 2002; Grenier and others, 2004). In fact, both white-tailed prairie dog and black-footed ferret numbers increased despite more than 10 years of active plague (Grenier and others, 2004).

Status of Prairie Dog Conservation

Since black-footed ferret recovery and prairie dog management issues are closely tied, the future of the black-footed ferret essentially depends on developing effective management of black-tailed, white-tailed, and Gunnison’s prairie dogs. The Black-tailed Prairie Dog Conservation Team (later just the Prairie Dog Conservation Team), which includes representatives from 12 State wildlife agencies, has been working since 1998 to develop effective conservation for prairie dogs. The team first developed the Black-tailed Prairie Dog Conservation Assessment and Strategy (Van Pelt, 1999), which was followed by an addendum called the Black-tailed Prairie Dog Multi-State Conservation Plan (Luce, 2003), a guideline for development of State black-tailed prairie dog management plans. Black-tailed prairie dog management plans have been completed in Colorado, Kansas, Montana, New Mexico, North Dakota, Oklahoma, and Texas. Draft management plans are moving toward finalization in South Dakota and Wyoming. Arizona has a draft management plan and is currently evaluating black-tailed prairie dog reintroduction, while Nebraska does not expect to continue development of a management plan.

The Black-tailed Prairie Dog Multi-State Conservation Plan includes several provisions that are important to black-footed ferret recovery, two areas of which are of the greatest significance. First, the objectives for occupied area, shown in table 3, indicate a commitment on the part of a majority of the States with black-tailed prairie dogs to increase the occupied area from 631,127 ha to 685,946 ha by 2011 (Luce, 2003). Second, the Multi-State Conservation Plan sets other target objectives for the United States as follows:

1. Maintain at least the current occupied area of black-tailed prairie dog habitat in the two complexes greater than 2,025 ha that now occur on and adjacent to Conata Basin-Buffalo Gap National Grassland, S. Dak., and Thunder Basin National Grassland, Wyo.
2. Develop and maintain a minimum of nine additional complexes greater than 2,025 ha (with each State managing or contributing to at least one complex) by 2011. A State could contribute to a 2,025 ha complex along a State boundary by cooperating with the adjacent State to manage part of the complex. A similar agreement could be developed between a State and a Native American tribe.
3. Achieve and maintain at least 10 percent of total occupied habitat in colonies or complexes greater than 405 ha by 2011.

Table 3. Estimates of historical, current, gross, and suitable black-tailed prairie dog (*Cynomys ludovicianus*) habitat, and the 10-year minimum habitat objective (Luce, 2003). Native American tribes in Montana, South Dakota, and North Dakota will set an occupied-area objective independent of the States.

State	Historical potential habitat[1] (ha)	Current occupied habitat[2] (ha)	Gross habitat[3] (ha)	Suitable habitat[4] and minimum 10-year objective[5] (ha)
Arizona	2,854,090	0	2,854	1,861
Colorado	11,077,916	255,596	110,779	103,588
Kansas	14,513,206	52,861	61,039	60,181
Montana	24,479,316	36,450	120,401	97,349
Nebraska	14,594,350	32,400	59,430	55,588
New Mexico	15,803,686	24,300	39,148	35,288
North Dakota	4,473,334	8,303	44,733	40,723
Oklahoma	8,750,479	26,007	28,702	27,806
South Dakota	11,851,333	64,800	88,339	80,786
Texas	31,829,943	79,785	125,933	118,717
Wyoming	8,937,378	50,625	75,524	64,059
Total	149,165,031	631,127	756,882	685,946

[1] Historical potential habitat = total potential habitat (not occupied habitat) encompassed within the range of the black-tailed prairie dog (as mapped by Hall, 1981). See Luce (2003) for further explanation.

[2] Current occupied habitat = estimates provided by the individual States.

[3] Gross habitat = total area of core range × 0.01 + area of secondary range × 0.001. Core range was defined as Bailey Ecosections dominated by shortgrass prairie plants and having black-tailed prairie dogs on the list of native fauna. Secondary range was defined as Bailey Ecosections dominated by plants not associated with shortgrass prairie, or having historically suitable habitat but a current sociopolitical climate unfavorable for prairie dog management. See Luce (2003) for additional details.

[4] Suitable habitat = gross habitat minus habitat with >10% slope and habitats such as large bodies of water, badlands, wetlands, forests, or other features not used by prairie dogs. Agricultural lands were included if they met the slope criterion.

[5] Minimum 10-year objective = objective for minimum area of occupied prairie dog habitat in each State, and total for the 11 States, by 2011.

4. Maintain distribution across at least 75 percent of the counties in the historical range or at least 75 percent of the historical geographic distribution. Ten States currently meet this objective (Arizona does not since the black-tailed prairie dog was extirpated), and all but Nebraska and Arizona have black-tailed prairie dogs in 100 percent of the counties in the historical range. This objective addresses the need to maintain all prairie dog colonies, whatever the size or location, throughout the range. State management plans will deal directly with management of complexes and individual, isolated colonies.

Management strategies for black-tailed prairie dogs on tribal lands were prepared for the Intertribal Prairie Ecosystem Restoration Consortium in January 2002 (T. Vosburgh, oral commun., 2003). The goal is to develop and implement management programs for the conservation of prairie dog habitat. These management strategies were revised on February 4, 2002, following review and comment from participating tribes, the U.S. Fish and Wildlife Service, and the Interstate Coordinator for the 12-State Prairie Dog Conservation Team. The consortium convened twice in 2002 and is working with other groups and agencies to move prairie dog management and conservation forward. The tribes have drafted plans to ensure that prairie dog populations and habitat are maintained. The Lower Brule and Fort Belknap Indian Reservations have final prairie dog management plans in place, and draft plans have been prepared for the Fort Berthold, Northern Cheyenne, Crow Creek, and Rosebud Indian Reservations.

The States of Wyoming, Colorado, Utah, and Montana developed a conservation assessment for the white-tailed prairie dog in 2005 (Seglund and others, 2005a), as did the States of Arizona, New Mexico, Colorado, and Utah for the Gunnison's prairie dog (Seglund and others, 2005b). When a conservation strategy is developed for the Gunnison's prairie dog, complexes of colonies will be identified, and other sites with black-footed ferret reintroduction potential may thus become apparent.

Summary and Recommendations

The black-footed ferret recovery program has faced and overcome several obstacles to reach the point where it is today. Foremost were capture of the wild population at Meeteetse, Wyo., captive breeding, development of release strategies, and release site identification based on habitat suitability and other factors. Given that those obstacles to success were overcome, I believe that, at the present time, continued progress on black-footed ferret recovery depends upon identification and active management of additional reintroduction sites. To that end, I identify 70 sites in the historical range of the black-footed ferret that might meet the biological and habitat suitability requirements for reintroduction of black-footed ferrets within 3–10 years, contingent upon directed management emphasis, State and Federal agency management priorities, and, if on private land, landowner concurrence based on agreements or incentives.

The Black-footed Ferret Recovery Implementation Team and Prairie Dog Conservation Team are encouraged to:

- Cooperate closely with State and Federal agencies and eight tribal governments to move toward the targets set in the Black-tailed Prairie Dog Multi-State Conservation Plan and State and tribal management plans.
- Assist the White-tailed and Gunnison’s Prairie Dog Working Groups to develop management plans for both species.
- Cooperate to evaluate the sites presented in this paper and develop strategies to begin management of as many sites as possible for black-footed ferret reintroduction within 10 years.
- Support and advance the High Plains Partnership landowner incentive program and/or other programs designed to bring about landowner participation in grassland species management.

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References Cited

Antolin, M.F., Gober, P., Luce, B., Biggins, D.E., Van Pelt, W.E., Seery, D.B., Lockhart, M., and Ball, M., 2002, The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation: Transactions of the North American Wildlife and Natural Resources Conference, v. 67, p. 104–127.

Biggins, D., 2003, Decline of a white-tailed prairie dog population near Meeteetse, Wyoming: Fort Collins, Colo., U.S. Geological Survey, Prairie Dog Research Update No. 8, 23 p.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Black-footed Ferret Advisory Team, 1990, A cooperative management plan for black-footed ferrets at Meeteetse: Cheyenne, Wyoming Game and Fish Department, 45 p.

Boschen, N.S., 1986, Black-footed ferret study in the Cisco Desert area of Utah, introductory report: Salt Lake City, Utah Division of Wildlife Resources, 21 p.

Cain, S.A., Kadlec, J.A., Allen, D.L., Cooley, R.A., Hornocker, M.G., Leopold, A.S., and Wagner, F.H., 1972, Predator control—1971: Ann Arbor, University of Michigan, Report to the Council on Environmental Quality and the Department of the Interior by the Advisory Committee, 207 p.

Chaplin, S.J., Ostlie, W.R., Schneider, R.E., and Kenney, J.S., 1996, A multiple-scale approach to conservation planning in the Great Plains, *in* Samson, F.B., and Knopf, F.L., eds., Prairie conservation—preserving North America’s most endangered ecosystem: Washington, D.C., Island Press, p. 187–201.

Clark, T.W., 1986, Some guidelines for management of the black-footed ferret: Great Basin Naturalist Memoirs No. 8, p. 160–168.

Clark, T.W., and Campbell, T.M., III, 1981, Additional black-footed ferret (*Mustela nigripes*) reports from Wyoming: Great Basin Naturalist, v. 41, p. 360–361.

Colorado Division of Wildlife, 2003, Conservation plan for grassland species in Colorado: Denver, Colorado Division of Wildlife, 38 p.

Conway, C.J., 1989, Evaluation of potential black-footed ferret reintroduction sites in Wyoming: Report prepared for the Wyoming Game and Fish Department, 10 p.

Cranney, S.J., and Day, K.S., 1994, 1993 prairie dog density surveys in the Diamond Mountain Resource Area: Vernal, Utah Division of Wildlife, Northeast Region, 8 p.

Cully, J.F., and Williams, E.S., 2001, Interspecific comparisons of sylvatic plague in prairie dogs: Journal of Mammalogy, v. 82, p. 894–905.

Cully, J.F., Jr., 1993, Plague, prairie dogs, and black-footed ferrets, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 38–49.

EDAW, Inc., 2000, Black-tailed prairie dog study of eastern Colorado: Report to the Colorado Department of Natural Resources, Denver, 31 p.

Ernst, A.E., 2001, Changes in black-tailed prairie dog towns on the Texas Panhandle determined by a geographic information system: Lubbock, Texas Tech University, M.S. thesis, 99 p.

Forrest, S.C., Clark, T.W., Richardson, L., and Campbell, T.M., III, 1985, Black-footed ferret habitat—some management and reintroduction considerations: Cheyenne, Wyoming BLM Wildlife Technical Bulletin No. 2, 49 p.

Grenier, M., Carpenter, A., Martin, M., Purcell, M., and Stephens, J., 2003, Black-footed ferret habitat evaluation of historical white-tailed prairie dog complexes in Wyoming, completion report, April 2003: Lander, Wyoming Game and Fish Department, 19 p.

Grenier, M., Van Fleet, L., and Oakleaf, B., 2004, Spotlighting for free-ranging black-footed ferrets in the Shirley Basin/Medicine Bow Management Area, Wyoming, *in* Cerovski, A., ed., Threatened, endangered, and nongame bird and mammal investigations, annual completion report: Lander, Wyoming Game and Fish Department, p. 19–35.

Hall, E.R., 1981, The mammals of North America (2d ed.): New York, John Wiley, 1,181 p.

Hansen, R.M., 1988, A chronology of prairie dog control operations and related developments in South Dakota, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: USDA Forest Service, General Technical Report RM-154, p. 121–122.

Hnilicka, P., and Luce, B., 1992, Habitat evaluation of the Shirley Basin/Medicine Bow black-footed ferret management area and selection of criterion for the premier reintroduction site, *in* Oakleaf, B., Luce, B., Thorne, E.T., and Torbit, S., eds., 1991 Annual completion report—black-footed ferret reintroduction, Shirley Basin: Lander, Wyoming Game and Fish Department, p. 39–51.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing mammal: Chicago, University of Chicago Press, 557 p.

Johnson, K., Neville, T., and Price, L., 2003, Remote sensing survey of black-tailed prairie dog towns in the historical New Mexico range: Albuquerque, New Mexico Natural Heritage Program, University of New Mexico, 28 p.

Kansas Black-tailed Prairie Dog Working Group, 2002, Kansas black-tailed prairie dog conservation and management plan: Pratt, Kansas Black-tailed Prairie Dog Working Group, 29 p.

Knowles, C.J., 2003, Status of the black-tailed prairie dog in North Dakota: Report prepared for the North Dakota Game and Fish Department, Bismarck, 56 p.

Lair, P., and Mecham, J., 1991, Black-footed ferret restoration evaluation/prairie dog status: Federal Aid report to the Texas Parks and Wildlife Department, WNM-KH-U, job no. 70, Aug. 31, 1991, 16 p.

Lomolino, M.V., and Smith, G.A., 2001, Dynamic biogeography of prairie dog (*Cynomys ludovicianus*) towns near the edge of their range: Journal of Mammalogy, v. 82, p. 937–945.

Lomolino, M.V., Smith, G.M., and Vidal, V., 2002, Long-term persistence of prairie dog towns—insights for designing networks of prairie reserves: Biological Conservation, v. 115, p. 111–120.

Luce, R.J., 2002, Black-footed ferret release site monitoring in Shirley Basin, Wyoming, *in* Brand, C.J., ed., Proceedings of an American Southwest Workshop—Landscape ecology of plague in the American Southwest, September 19–20, 2000, Fort Collins, Colo., p. 15.

Luce, R.J., 2003, A multi-state conservation plan for the black-tailed prairie dog, *Cynomys ludovicianus*, in the United States—an addendum to the Black-tailed Prairie Dog Conservation Assessment and Strategy, November 3, 1999: Sierra Vista, Ariz., Prairie Dog Conservation Team, 79 p.

Martin, D., and Luce, B., 1990, Black-footed ferret surveys, *in* 1990 Nongame program annual completion report: Lander, Wyoming Game and Fish Department, p. 30–38.

Miller, B., Reading, R.P., Forrest, S., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Miller, S.D., and Cully, J.F., Jr., 2001, Conservation of black-tailed prairie dogs (*Cynomys ludovicianus*): Journal of Mammalogy, v. 82, p. 894–905.

Montana Prairie Dog Working Group, 2002, Conservation plan for black-tailed and white-tailed prairie dogs in Montana: Helena, Montana Prairie Dog Working Group, 51 p.

Orabona-Cerovski, A., 1991, Habitat characteristics, population dynamics, and behavioral interactions of white-tailed prairie dogs in Shirley Basin, Wyoming: Laramie, University of Wyoming, M.S. thesis, 182 p.

Parrish, T.L., and Luce, B., 1990, Evaluation of potential black-footed ferret reintroduction sites in Wyoming: Laramie, Wyoming Cooperative Fish and Wildlife Research Unit and Wyoming Game and Fish Department, 14 p.

Seglund, A.E., Ernst, A.E., Grenier, M., Luce, B., Puchniak, A., and Schnurr, P., 2005a, White-tailed prairie dog conservation assessment: Laramie, Wyo., Western Association of Fish and Wildlife Agencies, 138 p.

Seglund, A.E., Ernst, A.E., and O'Neill, D., 2005b, Gunnison's prairie dog conservation assessment: Laramie, Wyo., Western Association of Fish and Wildlife Agencies, 87 p.

South Dakota Prairie Dog Work Group, 2001, Draft South Dakota black-tailed prairie dog management plan: Pierre, South Dakota Department of Game, Fish, and Parks, 77 p.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

U.S. Fish and Wildlife Service, 2000, 12-month finding for a petition to list the black-tailed prairie dog as threatened: Federal Register, v. 65, p. 5476–5488.

Vanderhoof, J.L., and Robel, R.J., 1992, Numbers and extent of black-tailed prairie dog towns in western Kansas. Final report—prairie dog population monitoring, habitat, attributes, and behavior: Contract no. 221, Kansas Department of Wildlife and Parks, 43 p.

Vanderhoof, J.L., and Robel, R.J., 1994, Numbers and extent of black-tailed prairie dog towns in Kansas: Transactions of the Kansas Academy of Science, v. 97, p. 36–43.

Van Pelt, W.E., 1999, The black-tailed prairie dog conservation assessment and strategy: Phoenix, Arizona Game and Fish Department, 55 p.

Wagner, D.M., and Drickamer, C., 2002, Distribution, habitat use, and plague in Gunnison's prairie dogs in Arizona: Heritage Grant I20009, report to the Arizona Game and Fish Department, 50 p.

A Habitat-based Technique To Allocate Black-footed Ferret Recovery Among Jurisdictional Entities

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Abstract

We offer a technique to allocate a hypothetical black-footed ferret (*Mustela nigripes*) recovery goal in an equitable fashion across the historical range of ferrets. A geographic information system (GIS) was used to predict the distribution of prairie dog (*Cynomys* spp.) habitat where the black-footed ferret historically occurred. Proportions of predicted habitat by jurisdictional entity provided a foundation to allocate a hypothetical delisting of the black-footed ferret. Subject to modification, this technique is presented as an example to bring long-term ferret recovery into finer focus at a national scale. In addition, we offer this technique to encourage a broader assessment of future reintroduction sites, to inspire creative thinking on how recovery goals could be allocated across the historical range, and to motivate collaborative efforts among Federal and State agencies, conservation groups, and private landowners to increase the likelihood of successful recovery of the black-footed ferret.

Keywords: black-footed ferret, *Cynomys*, geographic information system, GIS, *Mustela nigripes*, prairie dog, predicted habitat model, recovery

Introduction

The ultimate goal of the Endangered Species Act is recovery and subsequent preservation of threatened or endangered species (U.S. Fish and Wildlife Service, 2002a). Achievement of this goal can be defined in terms of downlisting, which is the reclassification of a species from endangered to threatened status, or delisting, which is the removal of a species from the Federal List of Endangered and Threatened Wildlife and Plants (Cole, 1989; U.S. Fish and Wildlife Service, 2002a). Downlisting and delisting result from successful recovery efforts; delisting occurs when protection of a species is no longer deemed necessary. To coordinate recovery efforts among Federal, State, and local agencies, the U.S. Fish and Wildlife Service prepares recovery plans that outline necessary procedures to achieve downlisting and delisting. Recovery plans identify specific tasks aimed at making a species a viable, self-sustaining component of its ecosystem (Cole, 1989; U.S. Fish and Wildlife Service, 2002b).

The first recovery plan for the critically endangered black-footed ferret (*Mustela nigripes*) was approved in 1978. At that time, no ferrets were known to exist in the wild (U.S. Fish and Wildlife Service, 1988; Cole, 1989). The subsequent discovery of a wild population of ferrets in Wyoming necessitated revision of the recovery plan. The main revision was a shift in management emphasis from free-ranging ferret populations to captive breeding and reintroduction (Biggins and Thorne, 1994). The revised recovery plan (U.S. Fish and Wildlife Service, 1988) placed the ferret program in a national scope and outlined steps “to ensure immediate survival of the black-footed ferret by: (1) increasing the captive population of black-footed ferrets to a census size of 200 breeding adults by 1991; (2) establishing a pre-breeding census population of 1,500 free-ranging black-footed ferret breeding adults in 10 or more populations with no fewer than 30 breeding adults in any population by the year 2010; and (3) encourage the widest possible distribution of reintroduced black-footed ferret populations” (U.S. Fish and Wildlife Service, 1988, p. 19).

As stated in the third step in the recovery plan, reintroduction of ferrets should be considered in the context of their historical geographic range. Selection of reintroduction sites should be based on several biological considerations, including the vulnerability of ferrets to demographic stochasticity (survival of population subgroups); environmental stochasticity (diseases, changes in predator densities); and genetic stochasticity (effects of inbreeding and loss of genetic variation through drift) (Shaffer, 1981; Groves and Clark, 1986; Clark, 1994). To be successful, however, black-footed ferret recovery must also involve more than biological considerations (Kleiman and others, 2000), and a variety of issues, including availability and ownership of potential habitat, should be considered when selecting reintroduction sites.

To date, selection of reintroduction sites has focused on identifying, protecting, and developing the most promising and

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largest reintroduction locations; however, large reintroduction sites may not be developed as rapidly as needed, and availability of these sites should not limit overall ferret recovery (Clark, 1994). New sites need to be identified, and maintenance of a few large sites should not necessarily preclude other, smaller recovery areas. To contribute to the overall recovery effort and to fulfill State recovery objectives, a strategy that incorporates recovery areas of various sizes would maximize the potential to secure ferret populations in the wild (U.S. Fish and Wildlife Service, 1988).

Additional challenges in ferret recovery include successful ferret reintroduction and effective long-term management of the sites (Reading and Miller, 1994). Selection of potential reintroduction sites is problematic and controversial and has suffered from disagreements among multiple interest groups, conflicting objectives, biological uncertainty, sociopolitical constraints, and intense public scrutiny (Maguire and others, 1988). Given these challenges, field biologists, veterinarians, and administrators representing Federal, State, and private agencies must provide a means by which to allocate ferret recovery in an equitable fashion. Equitable allocation will encourage participation by all entities and help place long-term ferret recovery in a national scope. To assist in meeting these challenges, we offer a habitat-based technique to allocate reintroduction efforts among jurisdictional entities. This technique is based on quantifying the relative amount of potential habitat across the geographic range. We offer this technique only as a test case to help bring long-term ferret recovery into finer focus at the national scale. Further, our technique will potentially broaden current assessments of future reintroduction sites and encourage cooperation across the extended network of people involved in the survival of the black-footed ferret.

Methods

Digital Data Layers

Recent advances in computer-aided mapping, combined with accessibility of geographic information system (GIS) data sets, enable production of digital maps depicting distributions of predicted habitat at a spatially detailed, landscape scale. Historical black-footed ferret specimens were recorded in association with three species of prairie dogs (*Cynomys* spp.), including the black-tailed prairie dog (*C. ludovicianus*), white-tailed prairie dog (*C. leucurus*), and Gunnison's prairie dog (*C. gunnisoni*) (Anderson and others, 1986). Further, black-footed ferret habitat is often defined in terms of prairie dog colonies. Thus, we created predictive habitat distribution models for the three species of prairie dogs. We defined and restricted the geographic area used in the predictive models by using the comprehensive prairie dog range maps as described by Hall (1981). These maps characterize the extremes of the area where prairie dog species were found historically and incorporate all known specimen records, including marginal habitats and disjunct populations. The range distribution maps provided by Hall (1981) were scanned with a desktop scanning device at 800 dots per inch. The digital images were saved in a tagged image file format to provide baseline GIS coverages. These images were registered to geographic coordinates, and distribution boundaries were digitized for each prairie dog species. We did not include the Utah prairie dog (*C. parvidens*) because evidence suggests that black-footed ferrets were not associated with this species (Anderson and others, 1986).

Collection records demonstrate that ferrets, until the first decades of the 20th century, were distributed over 40 million ha in 12 States and 2 Canadian Provinces (Anderson and others, 1986; Clark, 1986, 1987). County jurisdictional boundaries were acquired from the National Atlas of the United States® (http://www.nationalatlas.gov), imported into ArcGIS® 8.3 software (Environmental Systems Research Institute, Inc., Redlands, Calif.), and dissolved by State attributes, producing boundaries at a scale of 1:100,000 for the 12 States in which the black-footed ferret historically occurred.

Digital data sets depicting landscape attributes were chosen based on the availability and uniformity of data across the geographic range. We used the U.S. Geological Survey (USGS) National Land Cover Dataset (NLCD; http://landcover.usgs.gov/natllandcover.asp) to provide an estimate of current land cover. This data set depicts generalized land cover categories labeled agriculture, urban areas, forests, wetlands, grasslands, and shrublands with a 30-m spatial resolution. The NLCD was created from Landsat 5 Thematic Mapper satellite imagery digitally captured in 1992, produced by the Earth Resources Observation System Data Center. The NLCD was downloaded in complete State sections, which included a 300-m (10-pixel) buffer added to each outer State boundary. The data were then imported into ERDAS IMAGINE® 8.6 (Leica Geosystems Geospatial Imaging, LLC, Norcross, Ga.) and projected into a common coordinate system. Each State was clipped to the individual jurisdictional boundaries.

We used the USGS National Elevation Dataset (NED) to provide continuous, seamless elevation information at a 30-m spatial resolution. We downloaded the NED (http://ned.usgs.gov) in individual 1:250,000 quadrangles. The individual quadrangles were then map-joined to create one complete data layer for each State. Each data layer, as with all GIS data used in the model, was projected to a common coordinate system (Albers Equal Area projection). This projection is used in the United States and other countries that have a larger east-west than north-south extent because it preserves the area of the displayed features over the entire map with the same proportional relationship as the actual geographic areas they represent (Kennedy and Kopp, 2000). The individual data sets were then clipped to the State jurisdictional boundaries.

Predicted Habitat Models

We created digital models of predicted prairie dog habitat based on a set of landscape attributes and wildlife-habitat relationships. The wildlife-habitat relationships were based on attributes important in defining prairie dog habitat, such as land cover and topographic gradient (Koford, 1958; Clippinger, 1989). Generalized land cover categories considered suitable prairie dog habitat were grassland, shrubland, small grains, row crops, and pastures. Land cover types considered unsuitable were forests, water, and snow. Residential, wetland, and fallow land cover types may provide some prairie dog habitat; however, we considered these contributions minimal and placed these land cover types in the unsuitable category.

Topographic gradient was an additional landscape attribute used to predict prairie dog habitat. We used an algorithm in ERDAS IMAGINE 8.6 to derive percent slope from the NED. Slopes of 0–10 percent were considered suitable habitat. Although prairie dogs may occur on slopes greater than 10 percent, black-tailed prairie dogs usually build on slopes of less than 10 percent (Koford, 1958; Dalstead and others, 1981; Clippinger, 1989). Therefore, the remaining slope categories (11 percent and greater) were considered unsuitable habitat for all prairie dog species.

The Spatial Modeler module of ERDAS IMAGINE 8.6 was used to produce the individual predicted habitat models for each State. We used the additive overlay technique, which combined each individual data layer as an equally weighted component in the model. Although this process is referred to as additive, the file produced depicts the specific combination of the appropriate land cover and slope attributes selected as suitable prairie dog habitat. The predicted models for each State were then clipped to the individual range boundaries and merged into one complete data set. The result was a predicted habitat model for each prairie dog species.

The final step in modeling predicted habitat was removal of small, isolated tracts. Our models were produced at a 30-m spatial resolution, which we considered to be below the minimum habitat area required for black-footed ferrets. Minimum habitat area can be defined as the minimum amount of contiguous habitat that is required before an area will be occupied by a species (Clippinger, 1989). Because the different prairie dogs species afford different ferret carrying capacities, the size of suitable reintroduction areas ultimately depends on densities of prey. For example, ferrets have been shown to occur at densities of one adult black-footed ferret per 40–60 ha in white-tailed prairie dog colonies (Forrest and others, 1985; Richardson and others, 1986; U.S. Fish and Wildlife Service, 1988). Hillman and others (1979) found that 6 of 11 observed ferret litters occupied black-tailed prairie dog colonies greater than 40 ha. Further, black-tailed prairie dogs tend to be more gregarious and thus occur in more dense populations. Therefore, the minimum area of black-tailed prairie dog colonies that can support ferrets may be smaller than that for other prairie dog species (Clark, 1994).

We removed patches that were below the minimum size suitable for black-footed ferret survival in each habitat model with the Clump and Eliminate commands in ERDAS IMAGINE. We filtered predicted habitat based on the minimum area suitable for black-footed ferret survival. We used a minimum patch size of 40 ha in the black-tailed prairie dog range, 60 ha in the Gunnison’s prairie dog range, and 80 ha in the white-tailed prairie dog range.

Although the ability of various habitats to support populations of a given size will only be known from the results of reintroductions, at present it appears that large complexes are necessary for viable ferret populations (U.S. Fish and Wildlife Service, 1988). The minimum areas we chose may be reasonable based on available bioenergetic and behavioral information, however, and we offer them as working hypotheses in presenting our methodology for allocating ferret recovery.

Ferret Allocation

The 1988 recovery plan deferred specification of a delisting population size pending outcomes of reintroductions and accumulation of additional management experience (U.S. Fish and Wildlife Service, 1988). We offer a hypothetical delisting population size of 15,000 ferrets, an order of magnitude larger than the downlisting objective specified in the 1988 recovery plan. We chose this value based on several lines of reasoning. First, large prairie dog colonies such as those currently used for reintroductions may be scarce (Dobson and Lyles, 2000). Additional, smaller populations may be necessary to meet any delisting objective. Second, a larger number of smaller populations may help protect against catastrophic events (e.g., disease outbreaks) that can decimate entire populations (Forrest and others, 1988). Third, fossil evidence supports the hypothesis that black-footed ferrets may have been more common throughout the historical range (Linder and others, 1972; Choate and others, 1982; Hubbard and Schmitt, 1984; Anderson and others, 1986).

Although the majority of habitat occurs in the black-tailed prairie dog range, we suggest larger than proportional allocations of black-footed ferrets in the white-tailed and Gunnison’s prairie dog ranges. We suggest 8,625 ferrets (57.5 percent) allocated to the black-tailed prairie dog range; 3,375 ferrets (22.5 percent) to the Gunnison’s prairie dog range; and 3,000 ferrets (20 percent) to the white-tailed prairie dog range. To equitably divide ferret recovery across jurisdictional entities, we calculated the total amount of predicted habitat in the individual prairie dog ranges, calculated the percent of predicted habitat in each State, and then used those percentages to apportion black-footed ferrets by State and by prairie dog species.

Results and Discussion

Black-tailed Prairie Dog

Using the model described above, we calculated about 128.9 million ha of predicted habitat in the black-tailed prairie dog range (table 1), or about 71 percent of the range distribution as described by Hall (1981). The largest amount of predicted habitat occurred in Texas and encompassed over 29.2 million ha. New Mexico provided the second largest amount of predicted habitat with ~16.0 million ha. Nebraska, Kansas, and Montana had similar amounts of predicted habitat, with approximately 14 million ha each. North Dakota and Arizona, both considered range extremes, had the smallest estimate of predicted habitat with ~3.5 million ha and ~1.5 million ha, respectively. Texas was allocated 1,957 individual black-footed ferrets, and New Mexico was allocated 1,072 ferrets. South Dakota, where the last known extant populations of ferrets occurred in the black-tailed prairie dog range, was allocated 746 black-footed ferrets, and Wyoming was

Table 1. Amount of predicted habitat by prairie dog (*Cynomys*) species and jurisdictional entity, and resulting black-footed ferret (*Mustela nigripes*) allocations based on the hypothetical delisting objective of 15,000 individuals.

State	Predicted habitat (ha)	Percent of predicted habitat within each jurisdictional entity	Number of ferrets allocated	Minimum habitat required (ha)	Minimum habitat as a percent of total
Black-tailed prairie dog (*C. ludovicianus*)					
Arizona	1,484,257	1.2	99	3,960	
Colorado	9,870,127	7.7	660	26,400	
Kansas	13,977,156	10.8	935	37,400	
Montana	13,719,492	10.6	918	36,720	
Nebraska	14,660,668	11.4	981	39,240	
New Mexico	16,024,114	12.4	1,072	42,880	
North Dakota	3,520,025	2.7	236	9,440	
Oklahoma	7,764,139	6.0	520	20,800	
South Dakota	11,145,988	8.6	746	29,840	
Texas	29,248,634	22.7	1,957	78,280	
Wyoming	7,486,045	5.8	501	20,040	
Total	128,900,645	100.0	8,625	345,000	0.27
Gunnison's prairie dog (*C. gunnisoni*)					
Arizona	5,338,155	39.4	1,331	79,860	
Colorado	2,206,766	16.3	551	33,060	
New Mexico	5,505,857	40.7	1,373	82,380	
Utah	482,473	3.6	120	7,200	
Total	13,533,251	100.0	3,375	202,500	1.50
White-tailed prairie dog (*C. leucurus*)					
Colorado	934,483	8.9	268	21,440	
Montana	53,308	0.5	15	1,200	
Utah	1,075,817	10.3	309	24,720	
Wyoming	8,394,910	80.3	2,408	192,640	
Total	10,458,518	100.0	3,000	240,000	2.29

allocated 501. The State with the lowest ferret allocation was Arizona.

Based on our calculations (table 1), the minimum amount of habitat needed in the range of the black-tailed prairie dog was about 345,000 ha. Texas, with 23 percent of the predicted habitat, required a minimum of ~78,000 ha, and New Mexico required ~43,000 ha. Arizona could contribute ~4,000 ha. Overall, the minimum amount of habitat needed to achieve the hypothetical delisting objective was less than 1 percent of the total predicted habitat.

The amount of predicted habitat was calculated from input variables based on our model. We recognize that different definitions of suitable land cover could result in different amounts of predicted habitat and different ferret allocations. For example, we included agricultural land in our model based on the recognition that large areas of historically suitable prairie dog habitat were converted to cropland after settlement because prairie dogs prefer deep, relatively level soils—the same land preferred for agricultural development (Choate and others, 1982; Clark, 1986). Although we do not assume that land under current cultivation practices would be converted back to rangeland solely to provide black-footed ferret habitat, some agricultural practices may be compatible with black-footed ferret and prairie dog management, provided that prairie dogs can be tolerated (U.S. Fish and Wildlife Service, 1988). Overall, the agriculture class was approximately 44.7 million ha or 34 percent of the predicted habitat in the black-tailed prairie dog range. Oklahoma and Kansas had the largest proportions of agriculture, with more than 52 percent of the area under cultivation. In New Mexico, agriculture totaled over 48 percent of the area.

Gunnison's Prairie Dog

The amount of predicted habitat in the Gunnison's prairie dog range was over 13.5 million ha or 40 percent of the range distribution as described by Hall (1981). New Mexico had ~5.5 million ha of predicted habitat, followed closely by Arizona with ~5.3 million ha. Colorado had ~2.2 million ha of predicted habitat and Utah ~482,000 ha (table 1).

Based on our calculations, New Mexico and Arizona were allocated a similar number of black-footed ferrets, approximately 1,350 individuals. Colorado and Utah combined were allocated 671 ferrets. Our results indicate that the minimum amount of habitat needed to achieve the hypothetical ferret recovery goal was 1.5 percent of the total predicted habitat in the Gunnison's prairie dog range.

Unlike the black-tailed prairie dog range, inclusion of the agriculture land cover class did not have much impact in the Gunnison's prairie dog range. Only 5 percent of the area was estimated to be in agriculture; however, additional information, as it becomes available at a regional scale, might improve the model. For example, soil type, soil depth, and rock ground cover are important variables in defining Gunnison's prairie dog habitat (Wagner and Drickamer, 2004). These variables should be included in the model when the spatial data become available.

White-tailed Prairie Dog

White-tailed prairie dogs afforded the least amount of predicted habitat, ~10.5 million ha or 45 percent of the range distribution as described by Hall (1981). The majority of predicted habitat in the white-tailed prairie dog range occurred in Wyoming, which had over 8.3 million ha. Montana was estimated to have less than 1 percent of the total predicted habitat (table 1).

Based on our estimates (table 1), Wyoming could host 2,408 black-footed ferrets, Utah 309, Colorado 268, and Montana 15. Overall, in the white-tailed prairie dog range, the minimum amount of habitat needed to reach the hypothetical black-footed ferret recovery goal was 240,000 ha, with Wyoming contributing most of the potential habitat. The minimum amount of habitat estimated to achieve our hypothetical delisting objective was 2.3 percent of the total predicted available habitat.

As with the Gunnison's prairie dog predicted model, inclusion of agriculture did not strongly affect the outcome for white-tailed prairie dogs, with only 7 percent of the area classified in the agriculture land cover type; however, the white-tailed prairie dog model could be improved with more detailed land cover information. For example, the NLCD shrubland cover class may be too general to define white-tailed prairie dog habitat. Although white-tailed prairie dogs occur in shrubland habitats, shrub height and density (Collins and Lichvar, 1986) may be better predictive variables.

Distribution of Resources

Based on our model, Wyoming received the largest allocation of black-footed ferrets with approximately 2,909 individuals. New Mexico was allocated 2,445 individuals and Texas 1,957. The total amount of predicted habitat across all prairie dog species was 152.9 million ha. We calculated a minimum of 787,500 ha of habitat needed to attain the hypothetical delisting of the black-footed ferret, or less than 1 percent of the potential available habitat. Our results support the conclusion in the 1988 recovery plan that sufficient habitat to meet downlisting is less than 0.1 percent (75,000–100,000 ha) of western rangelands (U.S. Fish and Wildlife Service, 1988).

Conclusion

Our technique has several underlying assumptions. The principal assumption is that all prairie dog habitat is suitable black-footed ferret habitat. We recognize that black-footed ferret habitat is more restricted, requiring complex spatial configurations of prairie dog colonies, specific distances between those colonies, and substantial prairie dog densities (Stromberg and others, 1983; Houston and others, 1986; Biggins, Lockhart, and Godbey, this volume). Another assumption of our technique is that land cover data identified from modern remote sensing platforms can reasonably predict prairie dog habitat. Nevertheless, we offer this technique as a test case and encourage modifications and refinements. Future efforts should consider using a larger variety of input variables with more locally specific information, different classifications of land cover or slope categories, and greater spatial resolution.

Our technique (or refinements of it) could be used to allocate black-footed ferret recovery across jurisdictional entities. This technique may help place long-term black-footed ferret recovery into a national scope based on equitable contributions among those entities. In so doing we hope to inspire creative thinking on how specific recovery goals might be allocated across the historical range. We hope to motivate the collaborative effort among Federal and State agencies, conservation groups, and private landowners that will be needed to turn the black-footed ferret back from the brink of extinction (Cole, 1989; Reading and Miller, 1994).

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References Cited

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Biggins, D.E., and Thorne, E.T., 1994, Conservation management case studies, *in* Meffe, G.K., and Carroll, C.R., eds., Principles of conservation biology: Sunderland, Mass., Sinauer Associates, Inc., p. 368–374.

Choate, J.R., Boggess, E.K., and Henderson, F.R., 1982, History and status of the black-footed ferret in Kansas: Transactions of the Kansas Academy of Science, v. 85, p. 121–132.

Clark, T.W., 1986, Black-footed ferret—ghost of the prairie: Animal Kingdom, v. 89, p. 38–48.

Clark, T.W., 1987, Black-footed ferret recovery—a progress report: Conservation Biology, v. 1, p. 8–11.

Clark, T.W., 1994, Restoration of the endangered black-footed ferret—a twenty-year overview, *in* Bowles, M.L., and Whelan, C.J., eds., Restoration of endangered species—conceptual issues, planning and implementation: United Kingdom, University of Cambridge Press, p. 272–297.

Clippinger, N.W., 1989, Habitat suitability index models—black-tailed prairie dog: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 82(10.156), 21 p.

Cole, B.P., 1989, Recovery planning for endangered and threatened species, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 201–209.

Collins, E.I., and Lichvar, R.W., 1986, Vegetation inventory of current and historic black-footed ferret habitat in Wyoming: Great Basin Naturalist Memoirs No. 8, p. 85–93.

Dalstead, K.J., Sather-Blair, S., Worchester, B.K., and Klukas, R., 1981, Application of remote sensing to prairie dog management: Journal of Range Management, v. 34, p. 218–223.

Dobson, A., and Lyles, A., 2000, Black-footed ferret recovery: Science, v. 288, p. 985–988.

Forrest, S., Clark, T.W., Biggins, D., Richardson, L., Fagerstone, K., and Campbell, T.M., III, 1985, Life history characteristics of the genus *Mustela*, with special reference to the black-footed ferret, *Mustela nigripes*, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 23.1–23.14.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Groves, C.R., and Clark, T.W., 1986, Determining minimum population size for recovery of the black-footed ferret: Great Basin Naturalist Memoirs No. 8, p. 150–159.

Hall, E.R., 1981, The mammals of North America (2d ed.): New York, John Wiley, 1,181 p.

Hillman, C.N., Linder, R.L., and Dahlgren, R.B., 1979, Prairie dog distributions in areas inhabited by black-footed ferrets: American Midland Naturalist, v. 102, p. 185–187.

Houston, B.R., Clark, T.W., and Minta, S.C., 1986, Habitat suitability index model for the black-footed ferret—a method to locate transplant sites: Great Basin Naturalist Memoirs No. 8, p. 99–114.

Hubbard, J.P., and Schmitt, C.G., 1984, The black-footed ferret in New Mexico: Santa Fe, N. Mex., Bureau of Land Management, 118 p.

Kennedy, M., and Kopp, S., 2000, Understanding map projections—GIS by ESRI: Redlands, Calif., Environmental Systems Research Institute, Inc., 110 p.

Kleiman, D.G., Reading, R.P., Miller, B.J., Clark, T.W., Scott, J.M., Robinson, J., Wallace, R.L., Cabin, R.J., and Felleman, F., 2000, Improving the evaluation of conservation programs: Conservation Biology, v. 14, p. 356–365.

Koford, C.B., 1958, Prairie dogs, whitefaces, and blue grama: Wildlife Monographs, no. 3, 78 p.

Linder, R.L., Dahlgren, R.B., and Hillman, C.N., 1972, Black-footed ferret-prairie dog interrelationships, *in* Symposium on rare and endangered wildlife of the Southwestern United States: Santa Fe, New Mexico Department of Game and Fish, p. 22–37.

Maguire, L.A., Clark, T.W., Crete, R., Cada, J., Groves, C., Shaffer, M.L., and Seal, U.S., 1988, Black-footed ferret recovery in Montana—a decision analysis: Wildlife Society Bulletin, v. 16, p. 111–120.

Reading, R.P., and Miller, B.J., 1994, The black-footed ferret recovery program—unmasking professional and organizational weaknesses, *in* Clark, T.W., Reading, R., and Clarke, A., eds., Endangered species recovery—finding the lessons, improving the process: Washington, D.C., Island Press, p. 73–100.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1986, Black-footed ferret recovery—a discussion of some options and considerations: Great Basin Naturalist Memoirs No. 8, p. 169–184.

Shaffer, M.L., 1981, Minimum population sizes for species conservation: BioScience, v. 31, p. 131–134.

Stromberg, M.R., Rayburn, R.L., and Clark, T.W., 1983, Black-footed ferret prey requirements—an energy balance estimate: Journal of Wildlife Management, v. 47, p. 67–73.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

U.S. Fish and Wildlife Service, 2002a, Delisting a species—Section 4 of the Endangered Species Act: Arlington, Va., U.S. Fish and Wildlife Service, 2 p.

U.S. Fish and Wildlife Service, 2002b, Endangered species recovery program—frequently asked questions: Arlington, Va., U.S. Fish and Wildlife Service, 2 p.

Wagner, D.M., and Drickamer, L.C., 2004, Abiotic habitat correlates of Gunnison’s prairie dog in Arizona: Journal of Wildlife Management, v. 68, p. 188–197.

Habitat Restoration and Management

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Abstract

Black-footed ferrets (*Mustela nigripes*) historically occupied colonies of three prairie dog (*Cynomys*) species—Gunnison's (*C. gunnisoni*), white-tailed (*C. leucurus*), and black-tailed (*C. ludovicianus*)—more or less throughout their ranges. Historical declines in the abundance of ferret habitat (prairie dog colonies) resulted from poisoning of prairie dogs, sylvatic plague, conversion of habitat to agriculture, and changes in grazing practices to benefit mid-height and tall grasses. Prairie dog restoration often involves translocating prairie dogs into vacant habitat and managing vegetation to enhance colony growth. Sites for reestablishment should be selected with attention to ecological suitability, level of plague risk, return on economic investment in restoration and management, and social acceptability. Plague, conventional grazing and farming practices, and hostility of land managers toward prairie dogs can depress rates of restoration, but incentives may help overcome these obstacles. Two case histories illustrate restoration and management of black-tailed prairie dogs in two grassland types—mixed-grass and shortgrass. Options for expanding ferret habitat restoration and management opportunities include using small prairie dog complexes for ferret releases, introducing more intensive grazing to benefit black-tailed prairie dogs in taller grasslands, and reclaiming retired farmlands with shortgrass species beneficial to prairie dogs.

Keywords: black-footed ferret, *Cynomys* spp., habitat, management, *Mustela nigripes*, prairie dog, restoration

Introduction

Black-footed ferrets (*Mustela nigripes*) require populations of prairie dogs (*Cynomys* spp.) for sustained existence in the wild. Historical distribution records of ferrets coincide closely (though not exactly) with the presence of prairie dog colonies and the known historical ranges of three prairie dog species—black-tailed (*C. ludovicianus*), white-tailed (*C. leucurus*), and Gunnison's (*C. gunnisoni*). Ferrets collected outside prairie dog colonies or ranges could have come from ferret populations within colonies (Hubbard and Schmitt, 1984; Anderson and others, 1986). Efforts to recover ferrets proceed under the assumption that wild populations cannot long survive without prairie dogs (U.S. Fish and Wildlife Service, 1988).

Ferret habitat restoration thus implies restoration and management of prairie dogs, which of course requires suitable prairie dog habitat. Many landscapes historically occupied by black-tailed, white-tailed, or Gunnison's prairie dogs have been changed by conversion to agriculture, alterations in large herbivore abundance, or increases in woody vegetation. Singly or in combination, these changes have altered habitat suitability for prairie dogs (U.S. Fish and Wildlife Service, 2000; Knowles, 2002). Thus, habitat restoration for ferrets often must begin with habitat restoration and management for prairie dogs.

We focus herein on restoration and management of prairie dogs as a means of restoring ferret populations. First we discuss historical patterns of ferret and prairie dog abundance and, partly on that basis, regional priorities for restoration. Then we describe prairie dog restoration and management methods, challenges to both, and ways of expanding opportunities. Some issues, such as relative habitat quality among the prairie dog species, the influences of plague and predation, and the effects of livestock grazing, also are addressed elsewhere in this volume.

Ferret Habitat: A Historical Perspective

Historical information on ferret habitat is limited because of the fossorial and nocturnal habits of the species (Biggins and Schroeder, 1988) and its early demise. Even so, making the most of available data seems imperative; such data not only provide a rough template for restoration but also can inform the recovery process. The most reliable data primarily include past distributional abundance of ferrets based on verified records (usually collections) and the biogeographical patterns that can be inferred from these records. We recognize that collection records provide a poor surrogate for ferret abundance (numerous factors could influence collection density, as discussed later), but few other historical data sets are as relevant to restoration.

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The general picture that emerges from verified records shows a ferret distributional range largely overlapping the ranges of the three prairie dog species (fig. 1). Black-tailed prairie dog range, being much more extensive than ranges of white-tailed and Gunnison's prairie dogs, encompasses most of the ferret range and accounts for most of the ferret records (Powell, 1982; Anderson and others, 1986). An important question for restoration is whether these records suggest any apparent preferences of ferrets for prairie dog species or biogeographic regions.

If one assumes that density (number per unit area) of ferrets collected or otherwise verified in prairie dog range correlates with habitat quality or preference, Anderson and others' (1986) distribution maps in most cases suggest no clear preference among species within the same regions. Other factors, however, such as proportion of prairie dog range occupied by colonies, could confound judgments of habitat quality based solely on ferret records. Biggins, Lockhart, and Godbey (this volume) and Ernst and others (this volume) note the likelihood that higher density populations of prairie dogs supported more ferrets per unit area, and, as Knowles (2002) indicated, black-tailed prairie dogs usually occur in higher densities than do the other two species. New Mexico presents a conundrum (see also below) in that about four times as many ferret records came from Gunnison's as from black-tailed prairie dog range in the State (Anderson and others, 1986) despite the probable greater density of black-tailed prairie dogs and the estimated similarity in area occupied by the two species (see Hubbard and Schmitt, 1984).

The distribution of ferret records in black-tailed prairie dog range suggests that a greater density of ferrets occurred in northern parts than in southern parts. The northern half of the range produced about eight times as many ferret records as did the southern half (calculated from Anderson and others [1986]; fig. 1). Furthermore, numbers of ferret records from Montana, Texas, and the portion of New Mexico occupied by black-tailed prairie dogs (Anderson and others, 1986), viewed in light of estimated prairie dog colony area (table 1), show ferret records per habitat unit in Montana to be about 50 times those in New Mexico and well over 100 times those in Texas. Bailey (1905) described a single colony of black-tailed prairie dogs in Texas that occupied about 65,000 km^2; Anderson and others (1986) showed only two to five ferrets verified from the region occupied by that colony. In comparison, South Dakota's entire prairie dog range (including the unoccupied parts) covered only about twice that area but yielded 99 ferret records. Oklahoma, a southern State with roughly the same area of prairie dog range as that of South Dakota, yielded only four ferret records (Anderson and others, 1986).

Several factors other than habitat quality could have contributed to these north-south differences. Flath and Clark (1986) may have substantially underestimated the area of prairie dog colonies in Montana, and Bailey (1905) may have substantially overestimated it in Texas (D. Gober, oral commun., 2003). Trapping for furs, which accounted for some of the specimens collected (Anderson and others, 1986), may have been more intensive in areas producing better furs—that is, northern regions. The intrusion of agriculture into eastern portions of black-tailed prairie dog range may have occurred earlier in southern than in northern States, perhaps biasing

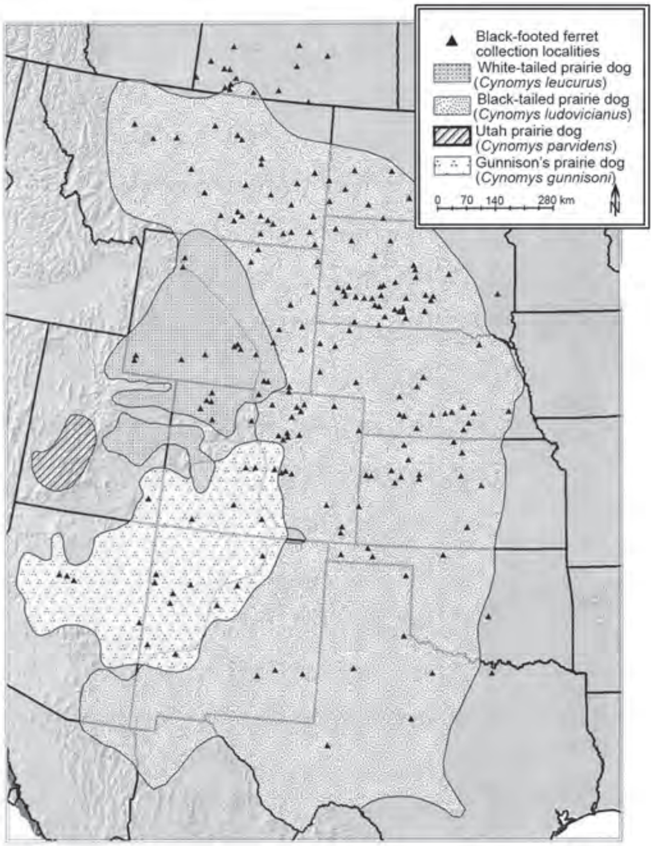

Figure 1. Collection locations for black-footed ferrets (*Mustela nigripes*) (Anderson and others, 1986) and historical ranges of prairie dogs (*Cynomys* spp.) across the Great Plains. Each collection location (dark triangle) represents $\geq$1 verified historical record(s).

Table 1. Black-footed ferret (*Mustela nigripes*) collection records from black-tailed prairie dog (*Cynomys ludovicianus*) range in three states, and densities of records within ferret habitat based on reported habitat acreages (i.e., areas occupied by prairie dog colonies).

State	Number of ferret records[a]	Estimated area (km^2) of habitat available	Ferret records/ 100 km^2 of habitat
Montana	44	6,000[b]	0.733
Texas	13	230,000[c]	0.006
New Mexico	3	~21,000[d]	0.014

[a] Anderson and others (1986).

[b] Flath and Clark (1986).

[c] Bailey (1905).

[d] Hubbard and Schmitt (1984).

later collection efforts toward northern States (Anderson and others, 1986). Finally, far southwestern (Chihuahuan Desert) portions of black-tailed range, having historically lacked large wild grazers (Truett, 1996), may have supported low numbers of prairie dogs (and few or no ferrets) prior to the proliferation of cattle (*Bos taurus*) (Hubbard and Schmitt, 1984).

Definitive answers about latitudinal differences in habitat quality of black-tailed prairie dog colonies will come only with comparisons between ferret releases that span the historical range. To date, colony complexes near Janos, Chihuahua, Mexico, host the only ferret releases in southern parts of black-tailed prairie dog range. The youth of this release program precludes a reliable assessment of its success.

Regional Priorities for Restoration

The Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) calls for establishing the widest possible distribution of 10 or more self-sustaining ferret populations. Sites for release of ferrets are selected on the basis of several criteria of habitat suitability (Biggins and others, 1993), key among which are size and expected longevity of prairie dog colony complexes. To complement this strategy, those planning prairie dog restorations probably should set regional priorities. We believe that important criteria for setting such priorities include level of plague risk, species of prairie dog, and regional differences in habitat quality within prairie dog species. All of these criteria will affect relative costs of prairie dog restoration and management.

Plague Risk

The sensitivities of prairie dogs and ferrets to plague make it the most important long-term threat to ferret habitat restoration in regions susceptible to epizootics. The historical spread of sylvatic plague eastward from the west coast and the apparent termination of this advance at the so-called plague line are addressed elsewhere (Cully and Williams, 2001; Gage and Kosoy, this volume). At present, plague apparently occurs in the wild more or less throughout the ranges of white-tailed and Gunnison's prairie dogs and in black-tailed range to about the western borders of South Dakota, Nebraska, Kansas, and Oklahoma—the plague line (Cully and Williams, 2001). The chances of plague epizootics affecting prairie dogs and ferrets west of the plague line seem to vary considerably among localities and to diminish as one nears the line.

Prairie Dog Species

Available evidence suggests to us that, among prairie dog species, the Gunnison's ranks lowest in priority for ferret habitat restoration and that the black-tailed ranks highest. We rank the Gunnison's prairie dog lowest primarily because of the species' relatively high and persisting losses rangewide to plague (Cully and Williams, 2001; Knowles, 2002) and its relatively intact (unaltered) habitat (Knowles, 2002); these factors suggest that restoration and habitat management efforts may lead to little long-term improvement in population status of the species. The average low survival and reproduction of ferrets released into a large Gunnison's prairie dog complex in Arizona (Conservation Breeding Specialist Group, 2004) suggest that, for unclear reasons, ferret habitat quality may be poor (plague appears to be absent at release sites).

We rank the white-tailed prairie dog second in priority. Although also at high risk from plague rangewide, this species is believed to suffer lower losses to epizootics than do Gunnison's or black-tailed prairie dogs, perhaps because of its commonly low population densities (Menkens and Anderson, 1991; Cully and Williams, 2001). In support of this belief, releases of ferrets during 1991–94 into a white-tailed prairie dog complex in Wyoming's Shirley Basin (Luce and others, 1997) resulted in unexpectedly high numbers of ferrets present in 2003 (Grenier, 2003), despite plague epizootics in the interim (Luce and others, 1997; Cully and Williams, 2001). Like Gunnison's prairie dogs, however, white-tails probably offer low per capita returns on investment in restoration and habitat management because of their low density and relatively intact habitat (Knowles, 2002).

We rank the black-tailed prairie dog highest in priority. A substantial proportion of their relatively large range remains plague free, densities within colonies (especially in plague-free areas) tend to be relatively high, and restoration and management efforts can yield high per capita returns. Much of the habitat within their historical range has been degraded, but substantial proportions could be restored. The most successful releases of ferrets have been in plague-free parts of black-tailed prairie dog range (Conservation Breeding Specialist Group, 2004).

Regions Within Black-tailed Prairie Dog Range

Priority for restoration varies from place to place within black-tailed prairie dog range. Most obviously, priority increases with decreased risk of plague. Ferrets released east of the plague line in South Dakota have survived and reproduced much better than those released west of the plague line in Montana (Conservation Breeding Specialist Group, 2004). Also, as noted above, if distributional abundance of ferret records correlates with habitat quality, restoration priority increases with latitude.

Restoration Methods and Challenges

We discuss two aspects of prairie dog restoration: reestablishment of populations and habitat improvement. Hostile traditions toward prairie dogs among land managers represent an important socioeconomic challenge to prairie dog restoration; incentives may help address this challenge.

Translocation

Timely restoration will require reestablishing prairie dogs where they formerly existed. At least three factors will hinder natural recolonization: (1) large spatial vacancies within previously occupied ranges, (2) short dispersal distances of black-tailed prairie dogs (Knowles, 1985) and probably the other species as well, and (3) infrequency with which new colonies originate on their own (Knowles, 1982). Translocations to establish new colonies will greatly accelerate the rate of restoration (D. Long and K. Bly-Honness, unpub. data, 2004).

Unlike natural colonization, translocation can space colonies across landscapes to form complexes ideal for ferrets and compatible with other land uses (see Bevers and others, 1997; Hof and others, 2002). Because small, new colonies expand much faster than large, old ones (Knowles, 1982; D. Long and K. Bly-Honness, unpub. data, 2004), translocation accelerates the rate of population growth. Also, translocation can retard or control unwanted expansion in source colonies by removing substantial proportions of the populations.

Only Utah prairie dogs (*C. parvidens*) and black-tailed prairie dogs have been extensively translocated (Truett and others, 2001a). Translocations of Utah prairie dogs commenced in the early 1970s with concern for the imperiled status of that species. Large-scale translocations of black-tailed prairie dogs have taken place primarily since 1990 (Long and others, in press). Methodologies for both species have been published elsewhere; below we review and compare these methods and recommend approaches that seem to work best for ferret habitat restoration.

Black-tailed Prairie Dogs

Source populations for translocating black-tailed prairie dogs should be selected with attention to disease risks, potential legal restrictions, genetic makeup, and effect of removal on the source population (Truett and others, 2001a; Long and others, in press). To date, plague presents the greatest disease problem and may indicate the need to quarantine animals (Marinari and Williams, 1998) before release. Monkeypox is an emerging disease issue but so far is confined to captive prairie dogs and other rodents. State or Federal restrictions on trapping and transporting prairie dogs may exist; recent restrictions related to monkeypox (U.S. Department of Health and Human Services, 2003) are the most prohibitive to date in that they restrict trapping and transport of all prairie dogs without special exemption. With respect to maintenance of unique gene pools, some biologists have voiced concern about translocating prairie dogs long distances. In practice this concern has influenced few translocation programs, although in New Mexico we acquired prairie dogs from a specific locality to help preserve the gene pool. Using translocations to remove unwanted animals is an attractive idea but in fact is an inefficient and often ineffective control method, in part because most populations seem able to support sustained harvests of at least 25–30 percent annually (T. Livieri, unpub. data, 2002).

The best sites for releases often have evidence of previous occupancy, but risk of plague or encroachment of tall vegetation may have degraded the suitability of such sites (Long and others, in press). Sites without evidence of historical occupancy also can be suitable if soils are deep and relatively fine textured and slopes are less than about 6 percent (Reading and Matchett, 1997). Grass dominance by grazing-resistant species is an important indicator of release site suitability (Long and others, in press).

Operators capture prairie dogs for translocation usually with livetraps but sometimes by pulling them from burrows with a vacuum truck or flushing them out with water (Truett and others, 2001a; Long and others, in press). We advise immediately treating captured animals with a pesticide to kill fleas, which can transmit plague, and then transporting them in wire-mesh cages to quarantine facilities or release sites. Important protocols for handling captive prairie dogs include protection from extreme temperatures, provision of adequate food and water, euthanization if seriously injured, and necropsy of any dying from unknown causes (Marinari and Williams, 1998).

We and most other practitioners conduct translocations during July–September to reduce losses of the very young that would occur with translocations in spring and to give released animals time to excavate new burrows before winter (Long and others, in press). We (Truett and others, 2001a; Long and others, in press) mow tall vegetation at release sites to 10 cm or less and hold the prairie dogs there for several days in acclimation cages consisting of belowground nest boxes connected by an access tube to aboveground retention baskets. The acclimation cages contribute greatly to survival by reducing dispersal and providing shelter from predators during the first few months postrelease while the prairie dogs are excavating new burrows. Predation by coyotes (*Canis latrans*) and badgers (*Taxidea taxus*) during this period usually accounts for most of the postrelease losses; installation of nest boxes at least 1.2 m deep, monitoring for predators at release sites for 2–3 weeks, and selective control of predators during this time commonly result in 50 percent or more surviving onsite at the end of 2 months. By that time, loss rates decline substantially. We usually see recruitment of young at near normal rates the following May and June.

In our experience, most operators translocate prairie dogs in groups as trapped without trying to retain them in original family units or specific sex and age groups. We found no significant difference in postrelease survival or recruitment between groups of prairie dogs translocated as family units ($n = 4$) and those translocated as mixed-family groups ($n = 6$) (Bly-Honness and others, 2004), but Shier (2004) found that five groups she translocated as family units survived and reproduced at higher rates than did five groups trapped without attention to family unity. We found (insignificantly) greater average survival among mixed-family groups translocated after being quarantined together for 2 weeks than among those not quarantined (Bly-Honness and others, 2004). Preliminary data indicated lower survival in groups containing more than about 60 percent juveniles than in groups containing less than about 40 percent juveniles (K. Bly-Honness and D. Long, unpub. data, 2004).

After several months, released animals have usually excavated numerous new secure burrows, and control of depredating coyotes and badgers becomes less important. Occasionally, large losses of prairie dogs at a release site will necessitate supplemental releases during the first several months after the initial release. Supplements usually survive at higher rates than those originally released because they take advantage of the burrows excavated by the first contingent. After several months to a year, management of colonies established by translocation differs little from management of preexisting colonies.

Other Prairie Dog Species

The relatively extensive work on translocation of Utah prairie dogs may instruct efforts to translocate white-tailed and Gunnison's prairie dogs. Utah prairie dogs are more closely related to these two species than are black-tailed prairie dogs, and they occupy similar habitats (i.e., intermountain valleys, benches, and plateaus; Knowles, 2002). Utah prairie dogs were first translocated in 1972, and approximately 20,000 individuals have been moved to date (Long and others, in press). In this section we focus on aspects of these translocations that are different from those discussed above for black-tailed prairie dogs. These differences are rather minor; they include primarily release-site selection and preparation and postrelease protection and monitoring.

Coffeen and Pederson (1993), citing Crocker-Bedford and Spillett (1981), provided criteria for release-site selection for Utah prairie dogs. Sites should be well drained, with soils at least 1.2 m deep and not easily collapsible. Vegetation should be sufficiently short or sparse to allow good horizontal visibility but sufficiently lush to provide forage even in dry periods. Evidence of previous occupancy by prairie dogs increases a site's suitability rating.

Treatment of release sites for Utah prairie dogs has primarily involved removal of tall, dense vegetation and augering of artificial burrows. Player and Urness (1982) demonstrated the benefits of shrub removal to postrelease survival; removal of plants that obstruct horizontal visibility has become standard practice (McDonald, 1993). Augered holes 9–15 cm in diameter and 0.5–1.0 m deep at angles into the ground provide relief from temperature extremes and some level of protection from predators (Player and Urness, 1982; Jacquart and others, 1986; McDonald, 1993). Covering entrances of augered holes with wire-mesh retention baskets to temporarily restrain the prairie dogs and acclimate them to the site (Player and Urness, 1982; Jacquart and others, 1986) appears to improve postrelease survival (McDonald, 1993).

As with black-tailed prairie dogs, mammalian predators, particularly badgers, apparently have caused the greatest losses in translocated Utah prairie dogs (Jacquart and others, 1986; Coffeen and Pederson, 1993; McDonald, 1993). Badger damage has been greatest during the first year or two following release, before the prairie dogs have excavated many secure burrow systems (Jacquart and others, 1986). In comparison, black-tailed prairie dogs usually seem secure from extensive badger depredation after several months (see above). Postrelease monitoring for predators and selective control of badgers are commonly used to protect Utah prairie dogs at release sites (Jacquart and others, 1986; Coffeen and Pederson, 1993). Even so, loss of released animals to badger predation remains a major problem (McDonald, 1993; D. Biggins, written commun., 2003).

Vegetation Management

For several reasons we address primarily black-tailed prairie dogs in this section. This species has a larger historical range that has been proportionately more degraded by agriculture and vegetation change than is the case with white-tailed and Gunnison's prairie dogs (Knowles, 2002). Absence of plague in substantial portions of black-tailed range, coupled with greater average densities of the species, increases the unit-area benefits of habitat restoration. Further, more information exists about habitat restoration and management for black-tailed than for white-tailed or Gunnison's prairie dogs, although the scarcity of information on the latter can be partly offset by the relatively rich database for the Utah prairie dog.

Prairie dogs respond markedly to habitat structure—soil texture, slope, and particularly vegetation height and density (Slobodchikoff and others, 1988; Reading and Matchett, 1997; Truett and others, 2001a). Short vegetation benefits all three species (Longhurst, 1944; Knowles, 1982; Slobodchikoff and others, 1988), presumably because it facilitates visual detection of approaching predators. Black-tailed prairie dogs seem more adversely affected by tall, thick vegetation than do Gunnison's or white-tailed prairie dogs (Scheffer, 1947; Hoogland, 1981; Hubbard and Schmitt, 1984). This effect may be a consequence in part of interspecific differences in predator avoidance behavior (Hoogland, 1981). Detection of predators by visual cues and intraspecific warning calls seem more highly developed in black-tailed prairie dogs, as does clipping of vegetation to improve visibility (Tileston and Lechleitner, 1966; Hoogland, 1996). These characteristics of this species may be evolutionary adaptations to exploit heavily grazed landscapes (Truett, 2003).

Many have noted the positive response of black-tailed prairie dogs to intensive grazing by large herbivores. Osborn and Allan (1949), Snell and Hlavachick (1980), Knowles (1982, 1986), and Cable and Timm (1988) documented expansion of colonies with heavy grazing and their stabilization or shrinkage without grazing in areas supporting mid-height or tall grasses. Truett and others (2001b) and Truett (2003) discussed historical fluctuations in abundance of black-tailed prairie dogs in Great Plains grasslands as a function of changing abundance of large grazers. Other ways of keeping the vegetation short, such as burning or mowing, can substitute for grazing (Ford and others, in press).

Only in shortgrass steppe, which occupies a relatively small part of their historical range (compare fig. 1 with fig. 2), do black-tailed prairie dogs seem relatively free of the need for large grazers (D. Long, unpub. data, 2004). In mixed-grass and tallgrass prairie, sustained absence of grazing (Osborn and Allan, 1949; Knowles, 1982), or simply grazing deferment during the growing season (Snell and Hlavachick, 1980; Snell, 1985), can within a few years or decades exclude black-tailed prairie dogs. This may hold true as well in many historically occupied sites in Chihuahuan Desert grasslands (Truett and Savage, 1998; J. Truett, unpub. data, 2004).

White-tailed, Gunnison's, and Utah prairie dogs tolerate tall, dense vegetation better than do black-tailed prairie dogs. Hoogland (1981) noted the relatively large numbers of shrubs in white-tailed prairie dog colonies (compared with black-tailed colonies) and thought they might serve as protective cover. Taylor and Loftfield (1924) and Longhurst (1944) noted the tolerance of Gunnison's prairie dogs for tall grasses and shrubs in their colonies. Collier and Spillett (1975) and Coffeen and Pederson (1993) indicated that Utah prairie dogs often coexist with, and may benefit from, shrubs.

Still, habitat quality for these species often appears to decline with increasing shrub density beyond some point. Longhurst (1944) described increasing density of Gunnison's prairie dogs with decreasing shrub density and increasing visibility. Collier and Spillett (1975) and the U.S. Fish and Wildlife Service (1991) attributed declines of Utah prairie dogs partly to historical increases in shrub density. As with black-tailed prairie dogs, these species may continue to face declining habitat quality unless tall vegetation (shrubs in this case) can be controlled. The federally threatened status of the Utah prairie dog has prompted attempts at habitat rehabilitation by "chopping" (Coffeen and Pederson, 1993), "rotobeating," "railing," and burning (Player and Urness, 1982) shrubs. Similar efforts to improve habitat for white-tailed and Gunnison's prairie dogs have not been reported.

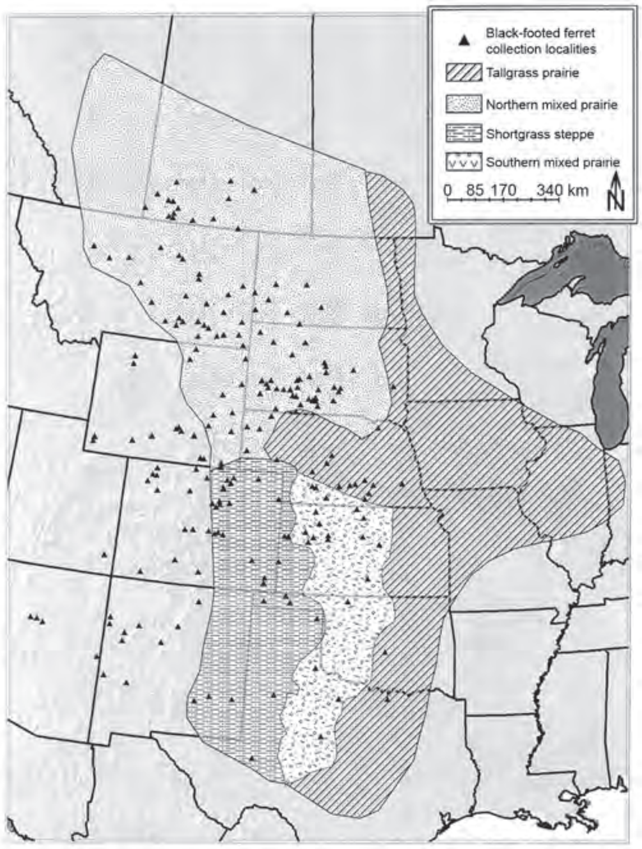

Figure 2. Collection locations for black-footed ferrets (*Mustela nigripes*) (Anderson and others, 1986) and distribution of Great Plains grassland types (Lauenroth and others, 1999). Each collection location (dark triangle) represents $\geq$1 verified historical record(s).

Socioeconomic Challenges

Aside from plague, the greatest impediment to prairie dog restoration may be hostile traditions among rangeland owners and managers. The historical demise of prairie dogs resulted in large part from control programs aimed at removing a presumed competitor with livestock (Merriam, 1902; Mulhern and Knowles, 1997). Perceptions molded by a century of institutionalized control of prairie dogs (Reading and others, 1999) will be difficult to reverse. To exacerbate the dilemma, livestock production on rangelands has long built on the tradition of moderate grazing uniformly distributed (Fuhlendorf and Engle, 2001), which, especially in mixed-grass and tallgrass prairie, militates against rapid restoration (Truett, 2003).

At a recent symposium on black-tailed prairie dogs, a Colorado rancher was asked why ranchers dislike prairie dogs. In response, he largely dismissed the risk of cattle breaking their legs in burrow entrances but pointed to the loss of forage that could reduce profits. Then, after some hesitation, he offered another important insight—prairie dog colonies simply look bad. Who wants to see his land blighted by the disturbed soil and rodent activity characteristic of prairie dog colonies? In word and gesture he portrayed prairie dogs as symbols of neglect, pariahs of the range, their presence a sign of lax stewardship comparable to an untidy house at Sunday dinner.

Independent of prairie dog control, grazing at light to moderate intensities has come to symbolize good land stewardship among range managers. To many, heavy grazing equates with "overgrazing" and unwise use. This perception took root in the early 1900s with Clements' (1916, 1936) model of "proper" grazing as that which maintained grasslands near climax condition (i.e., dominated by the tallest of the species at a given site). Historical evidence indicates that black-tailed prairie dogs thrived over the moister parts of their original range because of heavy grazing, first by bison (*Bison bison*) and then by cattle (Truett, 2003). Unfortunately for ferret restoration, the relatively moist and plague-free areas in the Great Plains that can support the greatest densities of prairie dogs need the heaviest grazing. Thus, black-tailed prairie dog restoration is squeezed between plague risks from the west and "good" range management from the east.

Managers' preferences for tall grass compromise another potentially fruitful avenue for prairie dog habitat restoration—reclamation of abandoned farmland (discussed later). The traditional maxim that tall grass is better grass leads most managers to recommend and use seed mixes containing largely tall or mid-height grass species for reclaiming lands such as those under the Conservation Reserve Program (CRP) of the 1985 Food Security Act.

In sum, those in the best position to restore prairie dogs on private and public lands usually lack the motivation to do so. They often come from rural backgrounds, which predisposes them to dislike prairie dogs (Reading and others, 1999). They subscribe to rural traditions that for generations have seen prairie dogs, and the range conditions associated with them, as economically and socially undesirable.

Given the entrenched nature of tradition, must changes in attitude await a new generation of managers with different cultural backgrounds? Perhaps not. For one thing, recent paradigm changes among professionals about what constitutes good conditions on rangelands (discussed later) may legitimize heavy grazing for conservation purposes (Task Group on Unity in Concepts and Terminology, 1995). A more immediate hope builds around incentives, particularly economic ones. Money has a history of reshaping tradition.

Incentives

Landowners, land managers, and agencies that set land management policy potentially can be motivated to restore prairie dogs through at least three kinds of incentives. The most direct and immediately effective incentive is probably economic—money offered to induce change. Regulation or the threat thereof can be brought to bear through the Endangered Species Act (ESA) or other legal means but may generate resentment and thus delay response. Self-motivated cultural change through education is slower still but usually longer lasting. Long-term success in prairie dog restoration may require a combination of all three strategies.

Economic incentives can come from private or public sources, and we can attest to the effectiveness of both. Turner Enterprises, Inc., and the Turner Endangered Species Fund (TESF) have supported prairie dog restoration on private ranches since 1995. Funding from TESF enabled restoration of prairie dog populations on six ranches and also promoted the concept of prairie dog restoration through educational efforts: technical publications, presentations at symposia and meetings, support of university graduate student programs, and field tours to educate people from grade schoolers through governors. Recently TESF funding has been supplemented by matching funds from nongovernment organizations (e.g., National Fish and Wildlife Foundation) and Federal agencies (e.g., U.S. Fish and Wildlife Service Private Stewardship Grants Program, or PSGP). The PSGP awarded grants for prairie dog restoration to other private landowners as well. In 2005, TESF received additional support through the new federally funded State Wildlife Grants Program as matching funds to assist with prairie dog restoration in South Dakota.

The U.S. Fish and Wildlife Service (2000) recently determined that the black-tailed prairie dog was warranted for listing as threatened under the ESA, listing being temporarily precluded by higher priority actions. This finding stimulated the States included in the species' historical range to collaborate on a conservation strategy (Luce and others, 2001). This strategy has involved a variety of actions including periodic meetings, interagency memoranda of understanding, and agreements on implementation schedules. Fear that management of the species would be assumed by the Federal government motivated this collaboration. The States organized working groups dedicated in part to planning and carrying out restoration actions, and many have completed population estimates and status assessments as a first step toward conservation (Luce and others, 2001). It is too early to assess the extent to which restoration on the ground will result from this action by the Federal government.

Over the longer term, the success of prairie dog and ferret restoration will rely on cultural acceptance of these species as valuable and appropriate components of grassland ecosystems. Private charities, Federal grants, and even government regulations that promote restoration all arose from cultural beliefs that more of nature should be preserved than just the parts generating income. All of these sources of support can disappear without consistent reinforcement of such beliefs. Maintenance of culture-based incentives will require a continuing effort to educate people about the intangible benefits of prairie dogs and other species that have little immediate economic worth. The most enduring incentives are likely to come through intergenerational transmission of values beyond money.

Case Histories

For several years the TESF has been restoring black-tailed prairie dogs on private ranches with the intent of eventually releasing ferrets into the habitat developed. Here we summarize restoration and management efforts on two of these ranches—Vermejo Park Ranch (Vermejo) in shortgrass prairie southwest of Raton, N. Mex., and the Bad River Ranches (Bad River) in mixed-grass prairie west of Pierre, S. Dak. Bison graze both ranches at generally moderate intensities.

Translocations to establish new colonies and protection of prairie dogs from poisoning and shooting have been key to restoration on both ranches. Most releases used source stock from within the respective ranches. Translocation methods followed Long and others (in press). Translocated animals were held for several days prior to release in acclimation cages at the release site; these cages had artificial underground nest chambers that prairie dogs continued to use after release while they excavated new burrows nearby. Predator control focused primarily on coyotes (both ranches) and badgers (Vermejo) during and for a few months following the translocation period. Major field efforts took place during May–October, involving one person on each ranch, with temporary help from another person for 2–3 months during June–August.

Vermejo

Annual monitoring of colony numbers and sizes commenced in 1997. Translocations began in 1999, and from then until 2003 we established 35 new colonies. Two colonies or fewer originated naturally during the 6-year period 1997–2003. Forty-six colonies currently exist, a few formed by the merging of two colonies that were originally separated.

Total area occupied by colonies increased from 202 ha in 1997 to 980 ha in 2003, expanding an average of 31 percent annually (mean of yearly values). Growth rate varied appreciably among colonies, mostly as a function of colony size. Colonies expanded an average of 12 percent per year during 1998–99 when a few large colonies predominated, but expansion increased to an average of 41 percent per year during 2000–03, during which time many small, new colonies were established by translocation.

The short-statured vegetation never seemed to offer much of an impediment to colony growth. Colony growth during 1999, when precipitation and vegetative growth substantially exceeded average, did not differ from that in 1998, when less rain fell. A major drought in 2001 and 2002 (21.8 cm and 23.9 cm, respectively, of precipitation compared with approximately 36.8 cm annual average) greatly reduced vegetative growth and recruitment of young into the prairie dog population but seemed not to influence areal expansion rate of colonies.

Bad River

Annual monitoring of colony numbers and sizes began in 1999, at which time 35 colonies existed. Translocations began in 2000, and from then until 2003 we established 35 new colonies. Eleven new colonies originated naturally during 1999–2003, mostly during a drought year (2002), and six disappeared during a wet year (2001). Seventy-eight colonies, a few having been formed by the merging of two original colonies, existed by late 2003.

Total colony area increased from 271 ha in 1999 to 584 ha in 2003; the average annual increase (mean of yearly values) was 25 percent. Smaller colonies grew faster than larger ones, but the greatest influence on colony growth resulted not from colony size but from grass height and density as a function of precipitation. In 2001, when rainfall and vegetative growth peaked, total colony area shrank 12 percent; in the drought year of 2002 colony area increased 72 percent.

Grazing by bison during years of average or above-average precipitation strongly influenced colony expansion. Heavily grazed colonies in these circumstances expanded at much greater rates than did colonies grazed lightly or not at all. Successful establishment of new colonies in wet years in the absence of grazing required us to mow release sites in summer, sometimes repeatedly, to enhance visibility and postrelease survival. Colonies in an area intensively managed—by establishment of new colonies, grazing at moderate intensities, and mowing as needed—grew 78 percent during the 2-year period that they were managed. Colonies outside this area grew by 29 percent during the same period.

Comparisons and Implications

Colony area in the shortgrass prairie at Vermejo expanded faster on average than that in the mixed-grass prairie at Bad River, and growth rate varied less among years at Vermejo. Our data suggest, however, that the potential average growth at Bad River with intensive grazing or drought may be substantially greater than that at Vermejo. This higher growth rate, coupled with the nearly threefold greater density of prairie dogs at Bad River (D. Long and K. Bly-Honness, unpub. data, 2004), illustrates the great potential that exists for ferret habitat restoration in taller grass regions of the Great Plains. Even so, it may be difficult to maximize this potential without changes in grazing management philosophy, which we discuss below.

Changing Paradigms, New Opportunities

Habitat scarcity seems a looming bottleneck in ferret restoration. The shortage of large prairie dog complexes suitable for ferret release coupled with the increase in ferrets annually available for release suggests a need to evaluate the use of smaller complexes. At the same time, changing philosophies and economics related to the major land uses in ferret range (i.e., grazing and farming) may open new avenues for habitat restoration and management. Below we assess some of the opportunities presented by these changes.

Minimum Size of Prairie Dog Complexes

Clearly, other factors being equal, larger complexes of prairie dog colonies offer better ferret habitat than do smaller ones. Although a high-density colony of black-tailed prairie dogs as small as 10 ha can in theory (Biggins and others, 1993) and in fact (Hillman and others, 1979) support a family of ferrets in the short term, Biggins and others (1993) recommended a minimum 400-ha colony area to sustain a ferret population. The Conservation Breeding Specialist Group

(2004) estimated that 2,440 ha of high-quality habitat (i.e., black-tailed prairie dog colonies in Conata Basin, S. Dak.) would be needed to support 120 breeding adult ferrets with more than 90 percent probability of persistence over 100 years. Moreover, they recommended development of 4,050-ha complexes to achieve ferret recovery objectives.

Given the current scarcity of large complexes secure from poisoning and plague, however, the Conservation Breeding Specialist Group (2004) also recommended investigating ways to enhance ferret recovery by using small (less than 2,000 ha) complexes. Use of smaller sites could attract collaborators (e.g., States and private landowners) excluded by large minimum-area requirements and quickly open up options spanning the entire historical ferret range. Literally and metaphorically, it could plant the seeds needed to ultimately establish larger complexes of prairie dog colonies and the widest possible distribution of ferrets.

Probabilities of extinction rise as ferret population size declines; thus, maintenance of ferrets in small colony complexes might necessitate periodic reintroductions from elsewhere. Still, this inconvenience might be trivial given the possible rewards—attracting wider public and private support, supplying wild-reared kits for release elsewhere, hosting research to better inform a variety of restoration schemes, and maintaining numerous wild populations as a hedge against regional catastrophe. Furthermore, finding ways to use small complexes could ultimately lead to shifts in grazing and farming philosophies to benefit ferret recovery.

New Directions in Grazing: Beyond Clements' Climax

Recently, members of the Task Group on Unity in Concepts and Terminology (1995) of the Society for Range Management laid to rest the conventional notion that grazing according to Clements (1916, 1936) (i.e., maintenance of grass communities near climax) is the sole gospel of good range management. They envisioned an array of potentially "good" grazing management options depending on management goals. In so doing, they legitimized such previously objectionable ideas as intensive grazing in areas of mixed-grass and tallgrass climax to benefit shortgrass species. In our view this change in perspective opened the door conceptually for extending prairie dog and ferret recovery efforts farther eastward into plague-free terrain.

Most ferret records for the Great Plains came from regions where prairie dog populations depended to some extent on grazing; that is, regions dominated by mixed or tall grasses (fig. 2) Historical accounts suggest that grazing by bison, before their demise in the 19th century, facilitated occupancy of these regions by prairie dogs and ferrets; the need for intensive and frequent grazing increased with distance eastward (reviewed by Truett, 2003). Bison had been eliminated in most Great Plains areas well before most ferret collections were made (cf. Anderson and others, 1986; Isenberg, 2000). Prior to bison extirpation, ferrets not only might have been more abundant in eastern portions of their range than numbers collected indicate, but also might have ranged farther east than ecologists have assumed.

Can intensive grazing (by livestock) be reinstated in these eastern, plague-free areas to pave the way for prairie dogs and ferrets? The historical rebound of prairie dogs in some of these areas following entry of cattle in very large numbers in the last decade or two of the 19th century (Merriam, 1902; Truett, 2003) suggests so. Several key management questions surround such a concept.

1. How far east can prairie dogs potentially thrive? Collection records (Hall, 1981) suggest that prairie dogs historically were common farther east than they generally occur now except under anomalous circumstances (e.g., predator-unfriendly sites such as remnant corners of pivot-irrigated fields or human settlements; Sidle and others, 2001; Truett, 2003). Some colonies established by people in high-rainfall areas east of historical range—for example, Nantucket Island off the coast of Massachusetts (Merriam, 1902) and a site east of Fort Worth, Tex. (Schmidly, 1983)—apparently have thrived. In the relatively cool and moist climate of the late Pleistocene, black-tailed prairie dog range extended substantially east of its historical limits (Goodwin, 1995), possibly because of heavy grazing by the numerous megaherbivores of the time (Truett, 2003). The key to prairie dog survival eastward to the limits of historical range and beyond may simply be short grass.

2. What vegetative changes come with the intensive grazing associated with prairie dog occupancy of mixed-grass and tallgrass sites? Mid-height and tallgrass species decline in dominance, often dramatically, and perennial shortgrasses and annuals increase (Detling, 1998; Truett and others, 2001b). Given availability of propagules, shortgrass species such as buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and tumblegrass (*Schedonnardus paniculatus*) increase and often persist in dominance (Archer and others, 1987; Weltzin and others, 1997). Net primary productivity (indicative of forage quantity annually available) typically declines over time, but forage quality increases. Heavy grazing by livestock outside colonies causes similar but usually less dramatic changes (reviewed by Truett and others, 2001b).

3. Would these changes reduce profits from ranching operations? The many variables involved preclude a detailed response, but the short answer is sometimes yes and sometimes no (Detling, 1998; this volume). Prime among the important variables is the proportion

of the landscape occupied by prairie dog colonies. Livestock profits may decline if prairie dog occupancy level is high but may increase if occupancy level is low. For example, Vanderhye (1985) projected substantial benefits to bison at a site in South Dakota where prairie dog colonies occupied only 12 percent of the landscape. Moreover, heavy grazing by cattle to benefit prairie dogs may under some conditions yield greater sustainable profits than would more conventional grazing intensities (Manley and others, 1997; Sims and Gillen, 1999).

Reclaiming Retired Farmland

Large proportions of the plague-free part of the Great Plains have been converted to agriculture; these proportions generally increase with distance eastward and southeastward (Lauenroth and others, 1999). Retirement of farm acreages under programs such as the CRP may offer the potential for prairie dog restoration. Could prairie dogs reoccupy retired farmlands? If so, how should reclamation of such lands proceed?

Black-tailed prairie dogs readily colonize abandoned farmland, often in preference to undisturbed prairie. In Montana, Knowles (1982) found that colonies were disproportionately abundant on previously cultivated lands near abandoned homesteads. In Colorado, Koford (1958) observed that prairie dogs near Fort Collins readily invaded fields under cultivation, and D. Seery (oral commun., 2002) noted that many prairie dog colonies on Rocky Mountain Arsenal National Wildlife Refuge, Colo., occupied long-abandoned fields. In Badlands National Park, S. Dak., Langer (1998) found more and larger prairie dog colonies on long-abandoned farmland than on undisturbed prairie. We observed that prairie dogs near Pierre, S. Dak., quickly invaded land last plowed the previous year.

As expected, cultivated land with tall vegetation repels prairie dogs; land with short or very sparse vegetation attracts them (Koford, 1958). Retired farmland reclaimed with perennial shortgrasses should sustain prairie dogs and, in some circumstances, limit erosion better than if tallgrasses were used in reclamation (see Truett, 2003), the latter a prime goal of the CRP. Mid-height and tall species of grass usually dominate CRP seed mixes (Reynolds and others, 1994; Johnson and Igl, 1995; Patterson and Best, 1996), however, rendering fields reclaimed with such mixes unsuitable for prairie dogs and other shortgrass fauna (e.g., see Kamler and others, 2003). Retired farmlands seem lucrative targets for prairie dog restoration, but seed mixes dominated by shortgrass species would be needed, particularly under programs such as CRP that limit grazing on lands enrolled in the program.

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References Cited

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Archer, S., Garret, M.G., and Detling, J.K., 1987, Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie: Vegetatio, v. 72, p. 159–166.

Bailey, V., 1905, Biological survey of Texas: Washington, D.C., U.S. Bureau of Biological Survey, North American Fauna No. 25, 222 p.

Bevers, M., Hof, J., Uresk, D.W., and Schenbeck, G.L., 1997, Spatial optimization of prairie dog colonies for black-footed ferret recovery: Operations Research, v. 45, p. 495–507.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Biggins, D.E., and Schroeder, M.H., 1988, Historical and present status of the black-footed ferret, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 93–97.

Bly-Honness, K., Truett, J.C., and Long, D.H., 2004, Influence of social bonds on post-release survival of translocated black-tailed prairie dogs (*Cynomys ludovicianus*): Ecological Restoration, v. 22, p. 204–209.

Cable, K.A., and Timm, R.M., 1988, Efficacy of deferred grazing in reducing prairie dog reinfestation rates, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 46–49.

Clements, F.E., 1916, Plant succession: Washington, D.C., Carnegie Institute Publication No. 242, 512 p.

Clements, F.E., 1936, Nature and structure of the climax: Journal of Ecology, v. 24, p. 252–284.

Coffeen, M.P., and Pederson, J.C., 1993, Techniques for the transplant of Utah prairie dogs, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 60–66.

Collier, G.D., and Spillett, J.J., 1975, Factors influencing the distribution of the Utah prairie dog, *Cynomys parvidens* (Sciuridae): Southwestern Naturalist, v. 20, p. 151–158.

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management planning workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

Crocker-Bedford, D.C., and Spillett, J.J., 1981, Habitat relationships of the Utah prairie dog: Logan, Utah, Report prepared by Utah Cooperative Wildlife Research Unit under U.S. Fish and Wildlife Service contract no. 14-16-0008-1117, 29 p.

Cully, J.F., Jr., and Williams, E.S., 2001, Interspecific comparisons of sylvatic plague in prairie dogs: Journal of Mammalogy, v. 82, p. 894–905.

Detling, J.K., 1998, Mammalian herbivores—ecosystem-level effects in two grassland national parks: Wildlife Society Bulletin, v. 26, p. 438–448.

Flath, D.L., and Clark, T.W., 1986, Historic status of black-footed ferret habitat in Montana: Great Basin Naturalist Memoirs No. 8, p. 63–71.

Ford, P.L., Anderson, M.C., Fredrickson, E.L., Truett, J.C., and Roemer, G.W., in press, Effects of fire and mowing on expansion of re-established black-tailed prairie dog colonies in Chihuahuan Desert grassland, *in* Narog, M.G., technical coordinator, Proceedings of the 2002 fire conference on managing fire and fuels in the remaining wildlands and open spaces of the southwestern United States: USDA Forest Service General Technical Report PSW-189.

Fuhlendorf, S.D., and Engle, D.M., 2001, Restoring heterogeneity on rangelands—ecosystem management based on evolutionary grazing patterns: BioScience, v. 51, p. 625–632.

Goodwin, H.T., 1995, Pliocene-Pleistocene biogeography of prairie dogs, genus *Cynomys* (Sciuridae): Journal of Mammalogy, v. 76, p. 100–122.

Grenier, M., 2003, Summary of black-footed ferret activities in Wyoming, 2003: Cheyenne, Wyoming Game and Fish Department, 1 p.

Hall, E., 1981, The mammals of North America: New York, John Wiley and Sons, 2 v., 1,175 p.

Hillman, C.N., Linder, R.L., and Dahlgren, R.B., 1979, Prairie dog distributions in areas inhabited by black-footed ferrets: American Midland Naturalist, v. 102, p. 185–187.

Hof, J., Bevers, M., Uresk, D.W., and Schenbeck, G.L., 2002, Optimizing habitat location for black-tailed prairie dogs in southwestern South Dakota: Ecological Modelling, v. 147, p. 11–21.

Hoogland, J.L., 1981, The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*): Ecology, v. 62, p. 252–272.

Hoogland, J.L., 1996, *Cynomys ludovicianus*: American Society of Mammalogists, Mammalian Species No. 535, p. 1–10.

Hubbard, J., and Schmitt, C., 1984, The black-footed ferret in New Mexico: Sante Fe, New Mexico Department of Game and Fish report to U.S. Bureau of Land Management, 118 p.

Isenberg, A.C., 2000, The destruction of the bison—an environmental history: Cambridge, U.K., Cambridge University Press, 206 p.

Jacquart, H.C., Flinders, J.T., Coffeen, M.P., and Hasenyager, R., 1986, Prescriptive transplanting and monitoring of Utah prairie dog (*Cynomys parvidens*) populations: Salt Lake City, Utah Division of Wildlife Resources, 70 p.

Johnson, D.H., and Igl, D.L., 1995, Contributions of the Conservation Reserve Program to populations of breeding birds in North Dakota: Wilson Bulletin, v. 107, p. 709–718.

Kamler, J.F., Ballard, W.B., Fish, E.B., Lemons, P.R., Mote, K., and Perchellet, C.C., 2003, Habitat use, home ranges, and survival of swift foxes in a fragmented landscape—conservation implications: Journal of Mammalogy, v. 84, p. 989–995.

Knowles, C.J., 1982, Habitat affinity, populations, and control of black-tailed prairie dogs on the Charles M. Russell

National Wildlife Refuge: Missoula, University of Montana, Ph.D. dissertation, 171 p.

Knowles, C.J., 1985, Observations on prairie dog dispersal in Montana: Prairie Naturalist, v. 17, p. 33–40.

Knowles, C.J., 1986, Some relationships of black-tailed prairie dogs to livestock grazing: Great Plains Naturalist, v. 46, p. 198–203.

Knowles, C.J., 2002, Status of white-tailed and Gunnison's prairie dogs: Missoula, Mont., National Wildlife Federation, and Washington, D.C., Environmental Defense, 30 p.

Koford, C.B., 1958, Prairie dogs, whitefaces, and blue grama: Wildlife Monographs, v. 3, p. 1–78.

Langer, T.J., 1998, Black-tailed prairie dogs as indicators of human-caused changes in landscape at Badlands National Park, South Dakota: Raleigh, North Carolina State University, M.S. thesis, 94 p.

Lauenroth, W.K., Burke, I.C., and Gutman, M.P., 1999, The structure and function of ecosystems in the central North American grassland region: Great Plains Research, v. 9, p. 223–259.

Long, D.H., Bly-Honness, K., Truett, J.C., and Seery, D.B., 2006, Establishment of new prairie dog colonies by translocation, *in* Hoogland, J.L., ed., Conservation of the black-tailed prairie dog: Washington, D.C., Island Press, p. 188–209.

Longhurst, W., 1944, Observations on the ecology of the Gunnison prairie dog in Colorado: Journal of Mammalogy, v. 25, p. 24–36.

Luce, B., Gober, P., Van Pelt, B., and Grassel, S., 2001, A multi-state, range-wide approach to black-tailed prairie dog conservation and management: Transactions of the North American Wildlife and Natural Resources Conference, v. 66, p. 464–479.

Luce, B., Oakleaf, B., and Williams, E.S., eds., 1997, Black-footed ferret reintroduction in Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, Annual Completion Report, 1996, 43 p.

Manley, W.A., Hart, R.H., Samuel, M.J., Smith, M.A., Waggoner, J.W., Jr., and Manley, J.T., 1997, Vegetation, cattle, and economic responses to grazing strategies and pressures: Journal of Range Management, v. 50, p. 638–646.

Marinari, P., and Williams, E.S., 1998, Use of prairie dogs in black-footed ferret recovery programs: Laramie, Wyo., U.S. Fish and Wildlife Service, National Black-footed Ferret Conservation Center, 8 p.

McDonald, K.P., 1993, Analysis of the Utah prairie dog recovery program, 1972–1992: Cedar City, Utah Division of Wildlife Resources, 81 p.

Menkens, G.E., Jr., and Anderson, S.H., 1991, Population dynamics of white-tailed prairie dogs during an epizootic of sylvatic plague: Journal of Mammalogy, v. 72, p. 328–331.

Merriam, C.H., 1902, The prairie dog of the Great Plains, *in* Yearbook of the United States Department of Agriculture, 1901: Washington, D.C., Government Printing Office, p. 257–270.

Mulhern, D.W., and Knowles, C.J., 1997, Black-tailed prairie dog status and future conservation planning, *in* Uresk, D.W., Schenbeck, G.L., and O'Rourke, J.T., technical coordinators, Conserving biodiversity on native rangelands—symposium proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-GTR-298, p. 19–29.

Osborn, B., and Allan, P.F., 1949, Vegetation of an abandoned prairie-dog town in tallgrass prairie: Ecology, v. 30, p. 322–332.

Patterson, M.P., and Best, L.B., 1996, Bird abundance and nesting success in Iowa CRP fields—the importance of vegetation structure and composition: American Midland Naturalist, v. 135, p. 153–167.

Player, R., and Urness, P., 1982, Habitat manipulation for reestablishment of Utah prairie dogs in Capitol Reef National Park: Great Basin Naturalist, v. 42, p. 517–523.

Powell, R.A., 1982, Prairie dog coloniality and black-footed ferrets: Ecology, v. 63, p. 1967–1968.

Reading, R.P., and Matchett, R., 1997, Attributes of black-tailed prairie dog colonies in northcentral Montana: Journal of Wildlife Management, v. 61, p. 664–673.

Reading, R.P., Miller, B.J., and Kellert, S.R., 1999, Values and attitudes toward prairie dogs: Anthrozoos, v. 12, p. 43–52.

Reynolds, R.E., Shaffer, T.L., Sauer, J.R., and Peterjohn, B.G., 1994, Conservation Reserve Program—benefit for grassland birds in the northern plains: Transactions of the North American Wildlife and Natural Resources Conference, v. 59, p. 328–336.

Scheffer, T.H., 1947, Ecological comparisons of the plains prairie-dog and the Zuni species: Transactions of the Kansas Academy of Science, v. 49, p. 401–406.

Schmidly, D.J., 1983, Texas mammals east of the Balcones Fault zone: College Station, Texas A&M University Press, 400 p.

Shier, D.M., 2004, Social and ecological influences on the survival skills of black-tailed prairie dogs (*Cynomys ludovicia-*

nus)—a role for behavior in conservation: Davis, University of California, Ph.D. dissertation, 90 p.

Sidle, J.G., Johnson, D.H., and Euliss, B.R., 2001, Estimated areal extent of black-tailed prairie dogs in the northern Great Plains: Journal of Mammalogy, v. 82, p. 928–936.

Sims, P.L., and Gillen, R.L., 1999, Rangeland and steer responses to grazing in the Southern Plains: Journal of Range Management, v. 52, p. 651–660.

Slobodchikoff, C.N., Robinson, A., and Schaack, C., 1988, Habitat use by Gunnison's prairie dogs, *in* Szaro, R.C., Severson, K.E., and Patton, D.R., technical coordinators, Management of amphibians, reptiles, and small mammals in North America: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-166, p. 403–408.

Snell, G.P., 1985, Results of control of prairie dogs: Rangelands, v. 7, p. 30.

Snell, G.P., and Hlavachick, B.D., 1980, Control of prairie dogs—the easy way: Rangelands, v. 2, p. 239–240.

Task Group on Unity in Concepts and Terminology, 1995, New concepts for assessment of rangeland condition: Journal of Range Management, v. 48, p. 271–282.

Taylor, W.P., and Loftfield, J.V.G., 1924, Damage to range grasses by the Zuni prairie dog: Washington, D.C., U.S. Department of Agriculture Bulletin No. 1227, 16 p.

Tileston, J.V., and Lechleitner, R.R., 1966, Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado: American Midland Naturalist, v. 75, p. 292–316.

Truett, J.C., 1996, Bison and elk in the American Southwest—in search of the pristine: Environmental Management, v. 20, p. 195–206.

Truett, J.C., 2003, Migrations of grasslands communities and grazing philosophies in the Great Plains—a review and implications for management: Great Plains Research, v. 13, p. 3–26.

Truett, J.C., Dullum, J.L.D., Matchett, M.R., Owens, E., and Seery, D., 2001a, Translocating prairie dogs—a review: Wildlife Society Bulletin, v. 29, p. 863–872.

Truett, J.C., Phillips, M., Kunkel, K., and Miller, R., 2001b, Managing bison to restore biodiversity: Great Plains Research, v. 11, p. 123–144.

Truett, J.C., and Savage, T., 1998, Reintroducing prairie dogs into desert grasslands: Restoration and Management Notes, v. 16, p. 189–195.

U.S. Department of Health and Human Services, 2003, Control of communicable diseases; restrictions on African rodents, prairie dogs, and certain other animals: Federal Register, v. 68, p. 62353–62369.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

U.S. Fish and Wildlife Service, 1991, Utah prairie dog recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, in cooperation with the Utah Division of Wildlife Resources, 41 p., 6 app.

U.S. Fish and Wildlife Service, 2000, Endangered and threatened wildlife and plants; 12-month finding for a petition to list the black-tailed prairie dog as threatened: Federal Register, v. 65, p. 5476–5488.

Vanderhye, A.V.R., 1985, Interspecific nutritional facilitation—do bison benefit from feeding on prairie dog towns?: Fort Collins, Colorado State University, M.S. thesis, 44 p.

Weltzin, J.F., Dowhower, S.L., and Heitschmidt, R.K., 1997, Prairie dog effects on plant community structure in southern mixed-grass prairie: Southwestern Naturalist, v. 42, p. 251–258.

Black-tailed Prairie Dog Interactions with Other Herbivores: Mediation via Alterations of Vegetation

By James K. Detling[1]

Abstract

Intensive grazing by black-tailed prairie dogs (*Cynomys ludovicianus*) typically reduces graminoid biomass and enhances production and standing crop of less desirable forage species; however, the quality of remaining graminoids is often increased because of higher crude protein concentrations and higher digestibility. Increased forage quality may partially account for why some large grazers such as bison (*Bison bison*), pronghorn (*Antilocapra americana*), and possibly cattle (*Bos taurus*) are attracted to prairie dog colonies as preferred sites to graze. In relatively productive grasslands, grazing and disturbance of tall vegetation by large herbivores apparently allow prairie dogs to expand into areas they might not otherwise occupy. These interactions between prairie dogs and large herbivores do not appear to be as strong in the more arid, less productive shortgrass steppe as in the mixed-grass prairie.

Keywords: bison, cattle, *Cynomys ludovicianus*, forage quality, grazing, plant-animal interactions, pronghorn, trophic interactions

Introduction

At the time that European settlers first migrated westward across North America, prairie dogs (*Cynomys* spp.) occupied vast areas of the Great Plains grasslands. For example, Merriam (1902, p. 258) described a single colony that occupied an area of nearly 65,000 km^2 and contained, by his estimate, 400 million prairie dogs. Much of the area originally inhabited by black-tailed prairie dogs (*C. ludovicianus*) is within the shortgrass and mixed-grass prairies, but they also occupy parts of desert grasslands and shrublands in southern New Mexico and northern Mexico (Hoogland, 1995; Detling, 2006). A large portion of their historical range is now either livestock grazing land or cultivated cropland. Because they can consume or destroy large quantities of forage by clipping, widespread eradication campaigns were mounted during the 20th century to eliminate prairie dogs from much of their original habitat. These campaigns, together with habitat loss and the introduction of bubonic plague into much of their former range, has resulted in an estimated 98 percent reduction in their populations from a century earlier (Miller and others, 1990, 1994). We now know that prairie dogs are important in the maintenance of grassland species diversity and are essential for survival of black-footed ferrets (*Mustela nigripes*) in the wild. Therefore, a number of ecologists and conservation biologists recently have argued for elimination of these eradication campaigns (Miller and others, 1990, 1994; Wuerthner, 1997; Kotliar and others, 1999), which has in turn raised concerns among land managers about how rapidly prairie dog populations might grow, what their effects on grassland vegetation might be, and how this might affect livestock or populations of native grazers.

This paper reviews extant literature pertaining to the above issues with respect to black-tailed prairie dogs. Specifically, I address three questions: (1) How does grazing by prairie dogs affect grassland vegetation? (2) What effects might these changes have on other herbivores? (3) How might grazing by other herbivores affect expansion of prairie dog colonies? Knowing the answers to such questions will enable us to better understand the nature of the habitat used by prairie dogs and associated species such as black-footed ferrets and will assist land managers in assessing some of the consequences of managing for increased area of prairie dog habitat.

Effects of Prairie Dogs on Vegetation

Vegetation Characteristics and Prairie Dog Diets

Most native shortgrass and mixed-grass prairies are dominated by perennial grasses and other graminoids, which may compose as much as 90 percent of the aboveground biomass (Coupland, 1992; Lauenroth and Milchunas, 1992). Although they typically make up a relatively low proportion of the biomass, a diverse group of forbs (i.e., herbaceous dicots) and woody sub-shrubs contribute substantially to overall plant species diversity in most Great Plains grasslands (Sims and others, 1978).

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Prairie dog diets consist largely of native graminoids, and many of the species they consume also compose most of the diets of native and domesticated ungulates (Detling, 2006). For example, on the shortgrass steppe of Colorado (Hansen and Gold, 1977) and the mixed-grass prairie of South Dakota (Uresk, 1984), relatively high-quality forage species such as blue grama (*Bouteloua gracilis*), needleleaf sedge (*Carex eleocharis*), western wheatgrass (*Pascopyrum smithii*), and sand dropseed (*Sporobolus cryptandrus*), all native perennial graminoids, made up about 85 percent of prairie dog diets. In contrast, forbs such as scarlet globemallow (*Sphaeralcea coccinea*) and a sub-shrub, fringed sagewort (*Artemisia frigida*), accounted for the other 15 percent. In addition to consuming vegetation, prairie dogs frequently clip and fell taller vegetation, apparently to enhance predator detection (Hoogland, 1995).

Changes in Plant Cover, Biomass, and Species Composition

As a result of their grazing and clipping behaviors, one of the most striking visual effects that prairie dogs have is a reduction in height of vegetation on their colonies. Where vegetation in uncolonized areas is relatively tall, the visual contrast between colonies and adjacent, uncolonized areas may be substantial. For example, at several mixed-grass prairie sites in South Dakota, vegetation adjacent to prairie dog colonies averaged about 25 cm tall while that on the colonies averaged <10 cm (Archer and others, 1987; Whicker and Detling, 1988a; Russell and Detling, 2003). Another common trend following colonization is a reduction in the amount of standing dead plant biomass relative to live biomass (Coppock and others, 1983a; Detling, 1998). Consequently, prairie dog colonies often appear “greener” than surrounding uncolonized grassland, reminiscent of classical “grazing lawns” (sensu McNaughton, 1984). In drier grasslands with shorter vegetation, such as the shortgrass steppe of eastern Colorado and northern New Mexico, differences in height of vegetation on and off colonies are much less dramatic (Guenther and Detling, 2003), and these colonies may not look greatly different from uncolonized grasslands.

As prairie dog colonies in the northern mixed-grass prairie age following initial colonization of a site, perennial graminoids become weakened by repeated leaf removal and the consequent reduction in their photosynthetic capacity. Not only is shoot biomass of graminoids reduced (Coppock and others, 1983a), but root biomass also declines markedly, particularly in older prairie dog colonies (Ingham and Detling, 1984; Whicker and Detling, 1988b; Detling, 1998). Consequently, over time graminoids lose their competitive dominance and are replaced by forbs and sub-shrubs (Coppock and others, 1983a; Archer and others, 1987). In Badlands National Park, S. Dak., for example, 7 of the 10 most abundant species sampled off prairie dog colonies were graminoids, while 8 or more of the most abundant species on old colonies were forbs (Fahnestock and Detling, 2002). Thus, prairie dog colonies may consist of a variety of vegetation types. Younger parts of colonies are grass dominated and have species composition similar to uncolonized sites but lower biomass and cover. The oldest, most altered parts of colonies are forb dominated and often have little or no graminoid cover or biomass. In addition, as colonies age, the proportion of bare ground tends to increase (Whicker and Detling, 1988b; Russell and Detling, 2003).

Less has been written about vegetation changes following colonization of southern mixed-grass prairie sites. At two >50-year-old colonies in Texas, biomass was only one-third to one-fourth as great on colonies as on uncolonized sites because mid-height grasses had been nearly eliminated (Weltzin and others, 1997a,b). In contrast to northern mixed-grass prairie sites, forb biomass was greater off colonies than on colonies, and biomass of short grasses did not differ significantly on and off colonies.

Available evidence suggests that vegetation is less altered by prairie dogs on the semiarid shortgrass steppe than in mixed-grass prairies. Nevertheless, the general trends appear to be in the same direction as in mixed-grass prairies. For example, in a shortgrass steppe in north-central Colorado, forb cover was greater (5.7 percent) on a colony than off it (3.4 percent), while cover of the dominant grass, blue grama, was lower on the colony (12.2 percent) than off it (19.2 percent) averaged over the growing season (Bonham and Lerwick, 1976). Similarly, Winter and others (2002) reported relatively small differences in vegetation structure and species composition on and off prairie dog colonies in shortgrass steppe in southwestern Kansas and southeastern Colorado. Moreover, bare ground was not significantly greater on colonies than off colonies at the Central Plains Experimental Range in northern Colorado (Guenther and Detling, 2003). These patterns of relatively small effects of prairie dogs on shortgrass steppe vegetation are consistent with the notion that this ecosystem has a long evolutionary history of grazing and is very resistant to heavy grazing (Milchunas and others, 1988), perhaps, in part, a result of the widespread dominance of grazing-resistant blue grama in this grassland type (Lauenroth and Milchunas, 1992).

Changes in Forage Quality

In addition to vegetation changes discussed above, grazing by prairie dogs may alter the phytochemistry and forage quality of plants. One such change involves nitrogen (or crude protein) concentration. In the northern mixed-grass prairie, mean live shoot [N] was 1.3 percent (crude protein = 8.1 percent) in six graminoid species off a prairie dog colony and 1.6 percent (crude protein = 10.0 percent) in the same six species on the colony when averaged over a growing season (Coppock and others, 1983a). Similar trends were observed by Krueger (1986). Moreover, the digestibility of graminoids was greater on prairie dog colonies than on uncolonized areas adjacent to them (Coppock and others, 1983a). Vanderhye's (1985) model results, reviewed by Detling (2006), suggested that changes in forage quality of the magnitude observed on these prairie dog colonies could significantly enhance weight gain of bison (*Bison bison*). Thus, heavy grazing by prairie dogs apparently results in a tradeoff: the quantity of forage species preferred by large grazers declines, but the forage quality of those species is enhanced. Determining the consequences of this quantity-quality tradeoff for cattle (*Bos taurus*) or other large grazers is complicated because the magnitude of the tradeoff likely depends on a variety of factors. These include the type of grassland, length of time a site was inhabited by prairie dogs, past and current management practices, weather conditions, and others. Nevertheless, some simple calculations based on data from a mixed-grass prairie site (Coppock and others, 1983a) might illustrate the approximate magnitude of this tradeoff.

Pringle Valley occupies 120 ha in Wind Cave National Park, S. Dak., and at the time of the study, prairie dogs occupied 36 ha (30 percent) of this valley (table 1). Coppock and others (1983a) recognized three zones within the colony based on length of time colonized: old colony (occupied >26 years), young colony (3–8 years), and edge of colony (<2 years). Since graminoids compose the majority of forage used by livestock, I calculated the effects prairie dogs had on mean growing season biomass, crude protein, and digestible dry matter of graminoids in the valley. These attributes of the forage differed as a function of time colonized (table 1). For example, at the colony edge, mean graminoid biomass per unit area was only 28 percent lower than on adjacent off-colony sites, while on the oldest part of the colony it was 98 percent lower. Because of the higher leaf [N] in plants on colonies (Coppock and others, 1983a), however, the mass of crude protein per unit area was only 12 percent lower at the colony edge (compared to 28 percent lower biomass) than at off-colony sites. Similarly, prairie dog-induced reductions in mass of crude protein in other zones of the colony were not proportionately as great as reductions in graminoid biomass, although they were greater than at the colony edge (table 1). Similar trends occurred for mass of digestible dry matter per unit area, but the magnitude of the compensatory effect was not as great (i.e., reductions in digestible dry matter more closely matched reductions in graminoid biomass) as it was for crude protein (table 1).

The quantity-quality tradeoff also can be illustrated by estimating the total reductions in mean biomass, mass of crude protein, and mass of digestible dry matter attributable to prairie dogs in the entire valley, rather than on a unit area basis (table 1). These estimates were made by multiplying the mass per unit area by the area in each zone of the prairie dog town (table 1) and comparing the totals with the quantity that would have been present if prairie dogs were absent (assuming the same values on the colony as were present in uncolonized grassland). Although the prairie dog colony occupied 30 percent of the area of Pringle Valley, seasonal mean graminoid biomass was only 17.5 percent lower in the valley with prairie dogs present than it would have been with no prairie dogs present, while masses of crude protein and digestible dry matter were 14.6 percent and 16.6 percent lower, respectively. Therefore, had this valley been a paddock on a ranch, available graminoid biomass would have been reduced by prairie dogs proportionately slightly more than available mass of crude protein or digestible dry matter. The difference in the proportional reductions in crude protein and digestible dry matter relative to reductions in biomass represents the approximate magnitude of the quantity-quality tradeoff. Thus, the compensatory effect of prairie dog grazing on forage quality was small compared to their effect on graminoid biomass. It should be stressed, however, that these reductions are greatest on the oldest part of the colony, which suggests that small, relatively young colonies, such as those in areas periodically killed by plague, may have only a small effect on carrying capacity for large grazing animals.

Responses of Other Herbivores to Prairie Dog-Induced Vegetation Changes

Native Herbivores

Some older literature suggests that large native herbivores such as bison and pronghorn (*Antilocapra americana*) may forage preferentially within prairie dog colonies (King, 1955; Koford, 1958). Most of this early literature was based on anecdotal observations and was not well documented with data; however, several subsequent studies have confirmed that such a positive association between large native herbivores and prairie dogs may occur, at least under some conditions.

In northern mixed-grass prairie, Coppock and others (1983b) examined bison use of prairie dog colonies at two different scales in Wind Cave National Park: (1) parkwide use of colonies and (2) use of a single colony in the 120-ha Pringle Valley. The parkwide study involved driving a given route through the entire park three to four times per week from mid-May through mid-October and comparing the proportion of all bison observed that were on colonies to the proportion of landscape occupied by colonies (12 percent). Bison use of prairie dog colonies was greatest during midsummer and, when in the western portion of the park that contained most of the colonies, bison strongly preferred colonies. When their movement patterns took them to the east side of the park (which had fewer colonies), however, bison did not show a preference for prairie dog colonies. Thus, prairie dog colonies did not solely control bison herd movement in the park.

The Pringle Valley study involved mapping, from a nearby fire tower, the location of each bison that entered the valley (Coppock and others, 1983b). When in the valley, bison used the prairie dog colony preferentially over uncolonized portions of the valley. From June through mid-October, they used graminoid-dominated parts of the town two to three

Table 1. Effects of colonization by black-tailed prairie dogs (*Cynomys leucurus*) on seasonal mean mass of graminoids, crude protein in graminoids, and digestible graminoid dry matter in Pringle Valley, Wind Cave National Park, S. Dak. Values were calculated from data on graminoid biomass, nitrogen concentration, and digestibility measured by Coppock and others (1983a) from June 1 to October 1, 1979.

	Off colony	Edge of colony	Young colony	Old colony	Total	% change by prairie dogs
Area occupied (ha)	84	12	15	9	120	-30
Mass per unit area (kg/ha)						
Live graminoids	990	710 (-28%)	410 (-59%)	20 (-98%)	---	
Crude protein	80	71 (-12%)	41 (-49%)	2 (-90%)	---	
Digestible dry matter	499	383 (-23%)	221 (-56%)	11 (-98%)		
Mass in each zone (kg/zone)						
Live graminoids						
Prairie dogs present	83,160	8,520	6,150	180	98,010	-17.5
If prairie dogs were absent	83,160	11,880	14,850	8,910	118,800	
Crude protein						
Prairie dogs present	6,757	852	615	18	8,242	-14.6
If prairie dogs were absent	6,757	965	1,207	724	9,653	
Digestible dry matter						
Prairie dogs present	41,916	4,596	3,315	99	49,926	-16.6
If prairie dogs were absent	41,916	5,988	7,484	4,491	59,879	

times as much as would be predicted by random utilization, and grazing was a predominant activity there. Following a fire in adjacent, uncolonized grassland, bison continued to use the prairie dog colony preferentially but also used the burned area preferentially over the remaining uncolonized, unburned portion of the valley (Coppock and Detling, 1986).

A subsequent study by Krueger (1986) at Wind Cave National Park confirmed and extended this research in several ways. First, in a parkwide study similar to that of Coppock and others (1983b), Krueger (1986) confirmed that bison used prairie dog colonies preferentially. From April through November, about 42 percent of all her bison observations were on prairie dog towns, which covered 12 percent of the sample area. Second, similar to results of Coppock and others (1983b), bison strongly preferred graminoid-dominated parts of colonies (96 percent of all observations) to forb-dwarf shrub-dominated areas (Krueger, 1986). Third, pronghorn also used prairie dog colonies (67 percent of all observations) more frequently than expected from random use (12 percent), and 79 percent of all pronghorn Krueger observed on prairie dog colonies were in areas dominated by forbs and dwarf shrubs. Thus, while bison and pronghorn both used prairie dog colonies preferentially, they made use of different vegetation zones and plant resources within the colonies.

The patterns described above may be modified by precipitation or other weather that affects resources available to grazers. For example, Green (1998) found that bison at Wind Cave National Park used graminoid-dominated parts of prairie dog colonies in proportion to their availability during a year of below average precipitation and forage production; however, in the following year when precipitation and forage production were above normal, bison used these areas preferentially. During the intervening winter, bison avoided prairie dog colonies.

Livestock

Are cattle and other livestock attracted to prairie dog colonies as bison and pronghorn apparently often are? This topic has not been thoroughly researched, so the answer is not clear. On the shortgrass steppe in northern Colorado, cattle used prairie dog colonies approximately in proportion to their availability; that is, they neither preferred nor avoided them (Guenther and Detling, 2003). While on these colonies, however, cattle grazed as intensively as they did in grassland communities not colonized by prairie dogs. Because the shortgrass steppe is quite different from the mixed-grass prairie, it is not possible to say whether the lack of a preference for colonies by cattle was the result of differences in foraging behavior between cattle and bison or differences in large ungulate (e.g., bison and cattle) grazing behavior on shortgrass steppe versus mixed-grass prairie. The result may be more closely related to differences in grassland type, since a year of average precipitation on the shortgrass steppe is similar to a dry year such as that observed by Green (1998) on the mixed-grass prairie.

While this latter idea is somewhat speculative and not supported by data, it is supported by anecdotal observations.

One such observation came in a letter addressed to me and postmarked March 30, 1998, from Mr. Francis Bardanouve, a former long-time member of the House of Representatives in Montana. Mr. Bardanouve was writing in response to statements attributed to me by Long (1998), in which I suggested that bison and pronghorn may graze preferentially on prairie dog colonies because of the higher quality forage there compared to uncolonized areas. Mr. Bardanouve, a self-described lifelong rancher from an area of mixed-grass prairie in northern Montana, wrote:

> I never really [saw] many [prairie dogs] until I began leasing lands on the Ft. Belknap reservation. In a few places it had towns [i.e., colonies] of several hundred acres…[Prairie dogs] cut everything off down to a height of almost less than an inch…There is no grazing left where they are.
>
> However, I have had one mystery which I could never explain. I suddenly realized the answer in your statement. From time to time I would occasionally move cattle within the lease for some reason. What I could never explain was I would be moving them along fine without any trouble until I hit a prairie dog town. It never failed the movement of the bunch [of cattle] would come to a screeching halt. The bunch would begin grazing grass so short you could hardly see it and I could hardly get them moving. I would move one side of the bunch ahead a little and the rest would not move. I would then rush over and shove them ahead and the part that I had just pushed would quit moving. This slow zigzag movement would continue until we were off the "town site" and then the herd would take off at their normal pace.

Clearly, such anecdotal observations should not be taken as scientific evidence that cattle in mixed-grass prairie are attracted to prairie dog colonies as bison or pronghorn are; however, accounts such as these lend some credence to the idea and could perhaps be used as a justification for future studies to address this question.

Does Grazing by Other Herbivores Affect Expansion of Prairie Dog Colonies?

By the early 1900s, settlers and their livestock had moved into much of the Great Plains, and to some it was evident that prairie dog populations were increasing. C. Hart Merriam (1902, p. 263), the former chief of the U.S. Bureau of Biological Survey, noted that "prairie dogs are now more abundant than formerly and their colonies have overspread extensive areas previously unoccupied." He attributed this increase to human-related factors, particularly (1) increasing the food supply for prairie dogs via cultivation of the soil and (2) decreasing the abundance of their natural enemies such as coyotes (*Canis latrans*), badgers (*Taxidea taxus*), hawks, owls, and snakes. Merriam (1902) recognized that prairie dogs caused substantial losses of forage and crops, but he apparently failed to consider that grazing and trampling of vegetation by settlers' livestock might have contributed to the rapid expansion of prairie dog populations.

By the mid-20th century, a number of researchers were beginning to recognize that large grazers might be responsible for expansion of prairie dog colonies. At the Wichita Mountains Wildlife Refuge in southwestern Oklahoma, Osborn and Allan (1949) studied a prairie dog colony that had been designated for complete protection from poisoning. Following termination of all cattle grazing permits in 1937, only native ungulates and a small group of longhorns grazed the 24,000-ha refuge, and very few grazed in the vicinity of this colony. Over the next decade, the study colony completely disappeared. Prairie dogs were known to be a shortgrass plains species and had previously been observed to spread into surrounding vegetation following overgrazing. Therefore, Osborn and Allan (1949) concluded that their initial presence on this site, whose natural climax vegetation was dominated by tall grasses, resulted from heavy grazing during its earlier use as cattle range. Following removal of cattle, they reasoned, grass cover increased in stature and density, and the prairie dogs were restricted to smaller and smaller areas until they eventually died out. By contrast, other colonies at the refuge persisted in spite of at least limited poisoning, but these colonies received regular grazing by bison and other big game (Osborn and Allan, 1949).

The idea that prairie dogs could expand more readily into short vegetation was supported by King's (1955) observations in the mixed-grass prairie of Wind Cave National Park. There, he observed that prairie dogs "invaded" a limestone outcrop covered with short vegetation about 100 m away from the parent colony rather than areas of taller vegetation adjacent to the existing colony. King (1955, p. 105) suggested "that short vegetation may encourage prairie dogs to settle a new area" and that they "seem to select vegetation that is neither too rank nor too tall" as they colonize new areas.

Following his study of prairie dog colonies in northern mixed-grass prairie, shortgrass steppe, and southern mixed-grass prairie, Koford (1958) also noted that prairie dog expansion was favored by shorter, less dense vegetation. In particular, Koford remarked (p. 63) that stands of tall grass surrounding prairie dog colonies could act as effective barriers to expansion, and that prairie dogs "seldom enter grass so tall and thick that they cannot see through or over it." Moreover, he noted (p. 65) that prairie dogs rarely expanded into rangeland that was in good to excellent condition and (p. 67) that "heavy grazing [by livestock] tends to reduce the barriers and allow the spread of prairie dogs." While Koford (1958, p. 67) felt that "conservative grazing" would allow vegetation to grow taller and inhibit prairie dog expansion, he also pointed out that this might not occur in more arid grasslands such as the shortgrass steppe. In support of this idea, Snell and Hlavachick (1980) observed that, after 4 years of rest from livestock grazing during the growing season in southern Kansas, native grasses on a prairie dog colony had become more abundant and the colony had decreased in area from about 45 ha to 5 ha.

Results from more recent studies are consistent with these earlier anecdotal observations and interpretations. For example, in northern mixed-grass prairie in South Dakota, Uresk and Bjugstad (1983) found an average of 106 active prairie dog burrows per hectare on sites where no cattle grazed and more than twice as many (235/ha) where cattle and prairie dogs grazed. They attributed the lower burrow density where cattle were excluded to taller vegetation there and concluded that high prairie dog densities were more likely to occur when rangelands are heavily grazed. In northeastern Montana, Knowles (1986) found that over 60 percent of the colonies he surveyed were on pastures with heavily grazed livestock developments and that nearly all (>97 percent) occurred adjacent to trails and roads. Interviews with landowners and managers suggested to Knowles (1986) that colonization of these areas by prairie dogs followed, rather than preceded, intensive grazing and soil disturbance. Likewise, Licht and Sanchez (1993) suggested that creation of cattle point attractants (e.g., water tanks and supplementary feeding sites) encourages colonization by prairie dogs after vegetation height around the attractants is reduced by livestock grazing and trampling. Similarly, Truett and Savage (1998) noted that expansion of introduced prairie dogs into Chihuahuan Desert grasslands typically only occurred where vegetation was less than 20–25 cm tall. Following mowing of taller vegetation, prairie dogs quickly moved into the mowed areas.

Scholarly reviews of the literature and early accounts of prairie dog interactions with large native and introduced herbivores such as bison and cattle led Truett and others (2001) and Truett (2003) to many of the same conclusions. Specifically, prior to extensive settlement of the Great Plains, the distribution of prairie dogs in more productive grasslands was closely linked to areas frequented by bison, which kept the grass relatively short. Following removal of bison, the range of prairie dogs shrank until cattle were introduced in large numbers, thereby allowing prairie dog populations to expand again. In areas where cattle were introduced soon after extermination of bison, prairie dogs persisted in large numbers; however, severe long-term overgrazing by livestock may reduce densities of prairie dogs by reducing availability of forage resources (Desmond, 2004).

Conclusions

The literature reviewed here suggests a strong interactive relationship between prairie dogs and other grazers, particularly in relatively productive grasslands. We have seen that, as a result of selectively grazing graminoids and clipping the vegetation to a short height, prairie dogs may greatly reduce aboveground plant biomass and cover, change plant species composition towards a greater dominance by forbs, and enhance the quality of the remaining forage via increases in leaf [N] and digestibility. Native grazers, such as bison and pronghorn, as well as cattle, may be attracted to these colonies as preferred sites to graze. Where densities of large grazers are relatively high, their grazing and trampling activities in uncolonized grassland may make some sites more suitable for colonization by prairie dogs and thereby facilitate expansion of prairie dog populations. While much of this latter concept is based on anecdotal reports rather than on experimental results, the preponderance of similar reports (Truett and others, 2001; Truett, 2003) lends credibility to it. In grasslands such as the semiarid shortgrass steppe, where vegetation is naturally shorter and dominated by species such as blue grama, the strength of many of the interactions between prairie dogs and large grazers discussed above is apparently not as strong.

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References Cited

Archer, S., Garrett, M.G., and Detling, J.K., 1987, Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie: Vegetatio, v. 72, p. 159–166.

Bonham, C.D., and Lerwick, A., 1976, Vegetation changes induced by prairie dogs on shortgrass range: Journal of Range Management, v. 29, p. 221–225.

Coppock, D.L., and Detling, J.K., 1986, Alteration of bison and black-tailed prairie dog grazing interaction by prescribed burning: Journal of Wildlife Management, v. 50, p. 452–455.

Coppock, D.L., Detling, J.K., Ellis, J.E., and Dyer, M.I., 1983a, Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity: Oecologia, v. 56, p. 1–9.

Coppock, D.L., Ellis, J.E., Detling, J.K., and Dyer, M.I., 1983b, Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs: Oecologia, v. 56, p. 10–15.

Coupland, R.T., 1992, Mixed prairie, *in* Coupland, R.T., ed., Ecosystems of the world. 8A. Natural grasslands. Introduction and Western Hemisphere: New York, Elsevier, p. 151–182.

Desmond, M., 2004, Effects of grazing practices and fossorial rodents on a winter avian community in Chihuahua, Mexico: Biological Conservation, v. 116, p. 235–242.

Detling, J.K., 1998, Mammalian herbivores: ecosystem-level effects in two grassland national parks: Wildlife Society Bulletin, v. 26, p. 438–448.

Detling, J.K., 2006, Do prairie dogs compete with livestock?, *in* Hoogland, J.L., ed., Conservation of the black-tailed prairie dog: Washington, D.C., Island Press, p. 65–88.

Fahnestock, J.T., and Detling, J.K., 2002, Bison-prairie dog-plant interactions in a North American mixed-grass prairie: Oecologia, v. 132, p. 86–95.

Green, R.A., 1998, Nitrogen distribution in a perennial grassland—the role of American bison: Fort Collins, Colorado State University, Ph.D. dissertation, 126 p.

Guenther, D.A., and Detling, J.K., 2003, Observations of cattle use of prairie dog towns: Journal of Range Management, v. 56, p. 410–417.

Hansen, R.M., and Gold, I.K., 1977, Blacktail prairie dogs, desert cottontails and cattle trophic relations on shortgrass range: Journal of Range Management, v. 30, p. 210–214.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing animal: Chicago, University of Chicago Press, 557 p.

Ingham, R.E., and Detling, J.K., 1984, Plant-herbivore interactions in a North American mixed-grass prairie. III. Soil nematode populations and root biomass on *Cynomys ludovicianus* colonies and adjacent uncolonized areas: Oecologia, v. 63, p. 307–313.

King, J.A., 1955, Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota: Ann Arbor, University of Michigan, Contributions from the Laboratory of Vertebrate Biology No. 67, 123 p.

Knowles, C.J., 1986, Some relationships of black-tailed prairie dogs to livestock grazing: Great Basin Naturalist, v. 46, p. 198–203.

Koford, C.B., 1958, Prairie dogs, whitefaces, and blue grama: Wildlife Monographs, no. 3, 78 p.

Kotliar, N.B., Baker, B.W., Whicker, A.D., and Plumb, G., 1999, A critical review of assumptions about the prairie dog as a keystone species: Environmental Management, v. 24, p. 177–192.

Krueger, K., 1986, Feeding relationships among bison, pronghorn, and prairie dogs—an experimental analysis: Ecology, v. 67, p. 760–770.

Lauenroth, W.K., and Milchunas, D.G., 1992, Short-grass steppe, *in* Coupland, R.T., ed., Ecosystems of the world. 8A. Natural grasslands. Introduction and Western Hemisphere: New York, Elsevier, p. 183–226.

Licht, D.S., and Sanchez, K.D., 1993, Association of black-tailed prairie dog colonies with cattle point attractants in the northern Great Plains: Great Basin Naturalist, v. 53, p. 385–389.

Long, M.E., 1998, The vanishing prairie dog: National Geographic, v. 193, no. 4, p. 116–130.

McNaughton, S.J., 1984, Grazing lawns—animals in herds, plant form, and coevolution: American Naturalist, v. 124, p. 863–886.

Merriam, C.H., 1902, The prairie dog of the Great Plains, *in* Yearbook of the Department of Agriculture (1901): Washington, D.C., U.S. Department of Agriculture, p. 257–270.

Milchunas, D.G., Lauenroth, W.K., and Sala, O.E., 1988, A generalized model of the effects of grazing by large herbivores on grassland community structure: American Naturalist, v. 132, p. 87–106.

Miller, B., Ceballos, G., and Reading, R., 1994, The prairie dog and biotic diversity: Conservation Biology, v. 8, p. 677–681.

Miller, B., Wemmer, C., Biggins, D., and Reading, R., 1990, A proposal to conserve black-footed ferrets and the prairie dog ecosystem: Environmental Management, v. 14, p. 763–769.

Osborn, B., and Allan, P.F., 1949, Vegetation of an abandoned prairie-dog town in tall grass prairie: Ecology, v. 30, p. 322–332.

Russell, R.E., and Detling, J.K., 2003, Grasshoppers (Orthoptera: Acrididae) and black-tailed prairie dogs (*Sciuridae: Cynomys ludovicianus* (Ord))—associations between two rangeland herbivores: Journal of the Kansas Entomological Society, v. 76, p. 578–587.

Sims, P.L., Singh, J.S., and Lauenroth, W.K., 1978, The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics: Journal of Ecology, v. 66, p. 251–285.

Snell, G.P., and Hlavachick, B.D., 1980, Control of prairie dogs—the easy way: Rangelands, v. 2, p. 239–240.

Truett, J.C., 2003, Migrations of grassland communities and grazing philosophies in the Great Plains—a review and implications for management: Great Plains Research, v. 13, p. 3–26.

Truett, J.C., Phillips, M., and Miller, R., 2001, Managing bison to restore biodiversity: Great Plains Research, v. 11, p. 123–144.

Truett, J.C., and Savage, T., 1998, Reintroducing prairie dogs into desert grasslands: Restoration and Management Notes, v. 16, p. 189–195.

Uresk, D.W., 1984, Black-tailed prairie dog food habits and forage relationships in western South Dakota: Journal of Range Management, v. 37, p. 325–329.

Uresk, D.W., and Bjugstad, A.J., 1983, Prairie dogs as ecosystem regulators on the northern high plains, *in* Kucera, C.L., ed., Proceedings of the Seventh North American Prairie Conference, August 4–6, 1980: Columbia, University of Missouri, Division of Biological Sciences, p. 91–92.

Vanderhye, A.V.R., 1985, Interspecific nutritional facilitation—do bison benefit from feeding on prairie dog towns?: Fort Collins, Colorado State University, M.S. thesis, 44 p.

Weltzin, J.F., Archer, S., and Heitschmidt, R.K., 1997a, Small-mammal regulation of vegetation structure in a temperate savanna: Ecology, v. 78, p. 751–763.

Weltzin, J.F., Dowhower, S.L., and Heitschmidt, R.K., 1997b, Prairie dog effects on plant community structure in southern mixed-grass prairie: Southwestern Naturalist, v. 42, p. 251–258.

Whicker, A.D., and Detling, J.K., 1988a, Ecological consequences of prairie dog disturbances: BioScience, v. 38, p. 778–785.

Whicker, A.D., and Detling, J.K., 1988b, Modification of vegetation structure and ecosystem processes by North American grassland mammals, *in* Werger, M.J.A, van der Aart, P.J.M., During, H.J., and Verhoeven, J.T.A., eds., Plant form and vegetation structure—adaptation, plasticity and relation to herbivory: The Hague, The Netherlands, SPB Academic Publishing, p. 301–316.

Winter, S.L., Cully, J.F., Jr., and Pontius, J.S., 2002, Vegetation of prairie dog colonies and non-colonized shortgrass prairie: Journal of Range Management, v. 55, p. 502–508.

Wuerthner, G., 1997, Viewpoint—the black-tailed prairie dog—headed for extinction?: Journal of Range Management, v. 50, p. 459–466.

Shooting Prairie Dogs

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Abstract

Recreational shooting of prairie dogs (*Cynomys* spp.) has occurred for many years, but interest and intensity have increased dramatically in the past decade. Shooting can cause prairie dogs to change their behavior and can affect sex and age groups differently. Prairie dog populations are capable of recovering from shooting or other reductions, but time to full recovery depends on demographic parameters (survivorship and fecundity). Simple population growth models with demographic variability demonstrate less risk of population extinction when shooting is regulated by effort rather than by quotas on numbers shot. Landowners might consider allowing shooting as a source of income, but, if not closely managed, shooters potentially can eliminate small colonies. Predation by black-footed ferrets (*Mustela nigripes*) probably does not significantly depress prairie dog populations. Prairie dog mortality caused by unregulated recreational shooting can vastly exceed predation by black-footed ferrets, affecting prairie dog survivorship and potentially affecting fecundity and recruitment. Until effects of shooting prairie dogs as prey for black-footed ferrets are better understood, shooting closures on reintroduction sites are appropriate.

Keywords: black-footed ferret, *Cynomys* spp., *Mustela nigripes*, prairie dog, recreational shooting

Introduction

Many long-time residents of western States recall spending summer vacations “plinking” prairie dogs (*Cynomys* spp.), whether by wrist rocket, air gun, or .22 caliber rifle. For over 100 years, shooting black-tailed prairie dogs (*C. ludovicianus*) in rural Kansas, for example, was common on Sunday afternoons by self-styled “varmint hunters” and by after-school target shooters (Smith, 1967). Shooting prairie dogs has been and continues to be primarily for sport but now involves marksmen who utilize high-technology rifles while practicing their shooting skills. To hone their skills, many shooters use a variety of rifles, scopes, range finders, shooting benches, and reloading equipment. Indeed, shooting prairie dogs at distances >450 m entitles one to membership in the 500 Yard Club, sponsored by the Varmint Hunters Association, and some members have registered successful shots >1,350 m.

Many shooters come from out of State (Vosburgh, 2000; South Dakota Prairie Dog Work Group, 2001), but this appears to be a recent phenomenon. In North Dakota, for example, nonresidents must purchase either a nongame license or a combination nongame and furbearer license to shoot prairie dogs; residents are exempt (North Dakota Game and Fish Department, 2001). The number of nonresident nongame licenses sold increased from 36 in 1975 to 625 in 2001, while nonresident nongame and furbearer license sales increased from 163 in 1989 to 1,326 in 2001 (S. Hagen, written commun., 2003). The recent increase in license sales to nonresidents in North Dakota indicates the rise in recreational shooting of prairie dogs by people from out of State. Similarly, in South Dakota over 35 percent of the estimated 16,011 prairie dog shooters on nontribal land in 2001 were nonresidents (Gigliotti, 2001).

Shooting Intensity

Available information indicates that substantial numbers of prairie dogs have been shot. In 2000, recreational shooters killed 1,186,272 prairie dogs on nontribal lands in South Dakota (South Dakota Prairie Dog Work Group, 2001). The number killed on nontribal lands increased to 1,516,174 in 2001 (Gigliotti, 2001). Shooters spent a total of 75,059 recreation days to kill that many prairie dogs: 54,849 by residents and 20,210 by nonresidents (Gigliotti, 2001).

During 1998 in Nebraska, 7,100 shooters spent 33,400 recreation days killing 301,000 prairie dogs; in 1999, fewer shooters (5,970) spent less time (28,300 recreation days) to kill more prairie dogs (356,000) (Nebraska Game and Parks Commission, 2001). The Colorado Division of Wildlife (2002) estimated (with ±95 percent confidence interval) that 6,070 shooters (±629) killed 418,412 prairie dogs (±75,234) during 64,674 recreation days (±825) in the 1998–99 reporting period. Based on these data, shooter success rates (number killed per recreation day) appear similar among reporting States: 6.5 killed per day in Colorado (between 5.2 and 7.7), 12.6 killed per day in Nebraska in 1999, and 20.3 killed per day in South Dakota in 2001.

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Estimates of prairie dogs killed in individual States depend on shooters' responses to survey questionnaires, which are possible only when shooters are licensed, such as in South Dakota and Colorado (South Dakota Prairie Dog Work Group, 2001; Colorado Division of Wildlife, 2002, 2003). On the other hand, nontribal recreational shooters on some tribal lands are required to be accompanied by a guide and must fill out a questionnaire that includes the number of days spent shooting, number of rounds fired, and estimated number of prairie dogs killed. In 2000, 936 shooters fired 156,307 rounds to kill 57,848 prairie dogs on the Rosebud Indian Reservation (T. Vosburgh, unpub. data, 2002). That rate of one prairie dog killed per 2.7 rounds fired is similar to an observed rate of one prairie dog killed per 3.0 shots fired on the Fort Belknap Indian Reservation in northern Montana during 2001 (Vosburgh, 2000).

The Lower Brule Indian Reservation in central South Dakota has collected 9 years of black-tailed prairie dog harvest data (table 1). From 1993 to 2001, an average of 121 licensed recreational shooters killed an average of 14,200 prairie dogs per year while spending an average of 372 recreation days on the reservation (Lower Brule Sioux Tribe, 2002). Each shooter averaged 118 prairie dogs shot per year or about 38 shot per day. That level of success is comparable to nonresident shooters on nontribal lands in South Dakota who, in 2001, spent an average of 3.5 days per shooter to kill 36 prairie dogs per day (Gigliotti, 2001). The average success rate was higher than reported above by Nebraska or Colorado. Relatively high levels of shooter success may be due to tribes' interest in recreational shooting as a source of revenue with concomitant monitoring of shooting effects on prairie dog populations. Also, out-of-State shooters may be especially diligent in pursuit of their quarry. During 2001, residents of South Dakota shot an average of 14 prairie dogs per day, considerably fewer than the 36 prairie dogs per day reported shot by nonresidents (Gigliotti, 2001).

Shooter success rates appear related to prairie dog densities. Typical densities of black-tailed prairie dogs exceed those of white-tailed prairie dogs (*C. leucurus*) (Tileston and Lechleitner, 1966), whereas densities of Gunnison's prairie dogs (*C. gunnisoni*) are intermediate or overlap those of the other two species (Fitzgerald and others, 1994). All three species are shot in Colorado, but harvest estimates are not reported by species, only by county (Colorado Division of Wildlife, 2003). Based on species' distributions (Fitzgerald and others, 1994), we estimated harvest for the three species (table 2). Although ranges of shooting success rates overlap, shooters in 2002–03 killed more prairie dogs per recreation day in counties with black-tailed prairie dogs than in counties inhabited by Gunnison's and/or white-tailed prairie dogs (table 2).

Effects of Shooting on Individual Prairie Dogs

Prairie dogs subjected to shooting change their behavior. In Montana, black-tailed prairie dogs in colonies with recreational shooting spent less time above ground than did prairie dogs in colonies with no shooting. When above ground, the former devoted less time to feeding and more time to scanning than the latter (Vosburgh and Irby, 1998). Prairie dogs in colonies with recreational shooting are more likely to escape when approached on foot or by vehicle, retreating to burrows sooner than prairie dogs not subjected to shooting (Vosburgh and Irby, 1998; Keffer and others, 2000). Increased alertness and early escape by prairie dogs are potential problems for recreational shooters, though some shooters may by more interested in shooting skill and firearm accuracy than in numbers of prairie dogs killed.

The timing of shooting prairie dogs may affect reproduction and mortality of various sex and age groups. Shooting from March to May is likely to kill pregnant or lactating females so that neither they nor their offspring will reproduce the following year (Knowles, 1988). Shooters generally cannot distinguish between male and female prairie dogs and, except during early summer, between adults and juveniles. Juvenile prairie dogs are more susceptible than adults to low levels

Table 1. Data from 9 years of shooting black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation, S. Dak.[a]

	Year								
Statistic	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**
Number of licenses sold	115	146	139	127	157	97	114	130	64
Estimated total killed	17,700	28,000	4,600	10,700	15,300	16,700	12,100	14,800	8,069
Total recreation days	367	503	334	486	372	392	363	319	211
Harvest/day/shooter	48	56	14	22	41	43	33	46	38
Average days/shooter	3.2	3.6	2.4	3.8	2.8	2.9	3.2	2.5	3.3

[a] Lower Brule Sioux Tribe (2002).

Table 2. Harvest estimates for three species of prairie dogs (*Cynomys*)—white-tailed (*C. leucurus*), Gunnison's (*C. gunnisoni*), and black-tailed (*C. ludovicianus*)—in Colorado during 2002–03 with rates and ranges of number killed per recreation day.

Species[a]	Number of counties in distribution[a]	Number of hunters[b]	Recreation days spent[b]	Total prairie dogs killed[b]	Shooter kill rate (number/day)	Range (number/day) for counties
White-tailed	5	1,063	13,197	30,943	2.34	0.78–5.51
White-tailed with Gunnison's	2	394	12,153	66,772	5.49	4.76−5.71
Gunnison's	12	827	9,278	31,533	3.40	0.00−6.44
Gunnison's with black-tailed	3	197	1,083	3,762	3.47	3.25−3.65
Black-tailed	20	1,948	17,845	170,867	9.58	1.42−101

[a] Counties within species' distributions as described by Fitzgerald and others (1994).

[b] Colorado Division of Wildlife (2003).

of shooting (Keffer and others, 2000). For example, when a colony having 35 percent juveniles was subjected to a 10 percent harvest during early to mid-summer, 53 percent of the animals killed were juveniles. On the same colony, adult females and adult males (39 percent and 26 percent of the population, respectively) were killed proportionately less than their occurrence in the population. Higher shooting pressure (>20 percent mortality) on another colony also targeted juveniles disproportionately (Keffer and others, 2000).

Adult females, including yearlings, appear more vulnerable to shooting than do adult and yearling males (Vosburgh and Irby, 1998; Keffer and others, 2000). During early summer 1995 in Montana, for example, the ratio of adult males to females was 92:100 on nine colonies (Vosburgh and Irby, 1998). In late summer, after an average of 8.5 hours of shooting per colony, the ratio of adult males to adult females was 167:100 on the same nine colonies. Survivorship of adult females during shooting was only 57 percent of the survivorship of adult males. On eight control colonies with no shooting, adult female survivorship was 122 percent of adult male survivorship between early and late summer in the same year (Vosburgh and Irby, 1998), which is similar to differential survival of unhunted black-tailed prairie dog populations elsewhere (Hoogland, 1995). Greater vulnerability of females probably exacerbates the impact of shooting by diminishing future reproduction.

Reproduction by adult and yearling female prairie dogs may be suppressed on colonies that are subject to continual recreational shooting. In North Dakota, only 32 percent of yearling female black-tailed prairie dogs on colonies disturbed by >20 years of heavy shooting reproduced (based on placental scars and evidence of ovulation) compared with 90 percent of yearling females on colonies relatively undisturbed by shooting (Stockrahm and Seabloom, 1988). Counts of placental scars in adult females ($\geq$2 years old) examined from the disturbed colonies were significantly lower than in adult females on relatively undisturbed colonies, indicating depressed reproduction on the disturbed colonies. These observations do not demonstrate that continual shooting was solely responsible for depressed reproduction because the disturbed colonies were spatially confined and not growing, whereas the undisturbed colonies were not spatially restricted and had doubled in size during the previous 5 years (Stockrahm and Seabloom, 1988). Depressed reproduction in the disturbed though confined colonies, especially by yearling females, may indicate density-dependent processes similar to those observed by Garrett and others (1982) in South Dakota.

Effects of Shooting on Prairie Dog Populations

Populations increase with birth and immigration of individuals but decrease with their death or emigration. For species such as prairie dogs that reproduce once a year (Hoogland, 1995) but die from various sources throughout the year, information about the rate of population increase (sometimes called the "finite rate of increase" and symbolized here by R; others often use lambda, λ) is important to understanding potential effects of recreational shooting on colonies. The equation $N_t = N_0 R^t$ can be used to compute population size at time t, N_t, if the initial population size, N_0, and R are known.

Finite rates of increase in prairie dog colonies with no shooting vary from year to year. For example, at one black-tailed prairie dog colony in Wind Cave National Park, S. Dak., colony size increased in some years but declined in others. Population finite rates of increase at this colony averaged 1.03 (1 standard deviation = 0.25), with minimum R = 0.70 and maximum R = 1.45 (Hoogland, 1995, table 16.1). Because this colony was surrounded by unsuitable habitat, its area remained constant, so the observed R = 1.0 might have been expected. Stationary populations often increase in response to factors such as addition of food, increase in habitable area, and population reduction (Caughley and Sinclair, 1994). Population reduction decreases competition, usually for food. With more food per individual, reproduction increases, mortality decreases, and the population grows (Caughley and Sinclair, 1994).

Limited experimental evidence demonstrates that removing prairie dogs, by shooting or other means, enhances population growth rates. After 2 consecutive years of shooting at two small black-tailed prairie dog colonies, populations were reduced or eliminated; in the year after shooting ceased, portions of both colonies were still inactive (Knowles, 1988). Five years after the shooting program ended, the larger of the two shot colonies had expanded to cover 140 percent of its preshooting area, and the smaller had grown to cover 90 percent of its former area (Knowles, 1988). Spatial growth of these treatment colonies resulted from increased numbers of prairie dogs, but details of population increase—whether by immigration from neighboring colonies or as a demographic response of the surviving prairie dogs—are unavailable. Data on active versus inactive burrow entrances indicate a similar response to cessation of shooting at larger black-tailed prairie dog colonies in South Dakota. Less than 45 percent of total burrows were active while recreational shooting was allowed, but, after 4 years without shooting, 74 percent of burrow entrances were active (B. Perry, unpub. data, 2000).

Rates of population increase have been documented under other conditions that reduce prairie dog populations. Knowles (1986) studied the effects of a toxicant, zinc phosphide, on several black-tailed prairie dog colonies by different treatment regimes and then observed the population recoveries for up to 5 years following the treatments. Knowles computed instantaneous growth rates for each year during population recovery. The instantaneous growth rate, r, is related to the finite rate of increase, R, by $R = e^r$, (Akçakaya and others, 1999) and is employed to predict population growth in continuous time rather than in discrete time, by the equation $N_t = N_0 e^{rt}$. One month after treatments that attempted to completely eradicate two colonies, Knowles (1986) estimated a reduction of 95 percent caused by the treatments. By continuing to monitor population recovery, Knowles computed average r = 0.916 (R = 2.499) after 1 year, r = 1.069 (R = 2.912) from the first to the second year and r = 0.350 (R = 1.419) from the second to the fifth year. For the five colonies that received partial toxicant treatment, which reduced target populations to an average of 19 percent of pretreatment levels, average r = 1.339 (R = 3.815) after 1 year and r = 0.148 (R = 1.160) from the first to the second year (Knowles, 1986).

Values for R reported by Knowles (1986) were higher for both study groups after the first year following treatments than values observed on a prairie dog colony in Wind Cave National Park, S. Dak. That colony expanded from 0.47 ha to 1.86 ha over a 3-year period (Garrett and Franklin, 1988) when colony size in June increased from 51 to 134 adults and juveniles (average R = 1.38). Similarly, a black-tailed prairie dog colony near Nunn, Colo., with no population reduction treatment, expanded from 2.1 ha to 3 ha in 1 year as the colony size in June grew from 28 to 82 animals (Koford, 1958, p. 10, table 1). For that colony in that 1-year period, R = 2.93, but in the previous year the colony had declined from 50 to 28 animals (R = 0.56).

Population responses were also tracked following reduction of two colonies in South Dakota by translocating live-trapped black-tailed prairie dogs (Radcliffe, 1992). After intensive removal during June of the first study year, 6 prairie dogs remained in one of the colonies, but 10 were present by June of the following year. By June of the second year following removal, the population had increased to 51 prairie dogs, but the increase was mostly attributed to immigration (Radcliffe, 1992). The second colony also grew substantially after the population was reduced to 10 individuals in June of the treatment year. By the next June that colony had grown to 23 and by June of the second year had grown to 80 prairie dogs; the extraordinary growth rate during the second year was R = 3.48. In this second colony, immigration played a minor role (three immigrated annually). Population growth mainly resulted from increased litter size and higher juvenile survivorship (Radcliffe, 1992).

These data support our earlier generalization that populations can be stimulated to grow by reducing the number of animals that compete for a limited resource. Similar population responses were noted in colonies of Gunnison's prairie dog during and after a sylvatic plague epizootic in Moreno Valley, N. Mex. Cully (1997) found that after plague killed more than 99 percent of the population, the few surviving prairie dogs formed two colonies in areas that were previously unoccupied. Using Leslie matrix analysis involving demographic parameters (survivorship and fecundity), Cully found that the population would be nearly tripling each year. The key to this high rate of population growth was found to be yearling females reproducing at a rate similar to that of adults and having a relatively high survival rate (Cully, 1997). Similarly, the survival rate of juveniles (90 percent) in a young, expanding black-tailed prairie dog colony in South Dakota was significantly higher than juvenile survivorship (49 percent) in an older, nonexpanding colony (Garrett and others, 1982). In addition, yearling females on the younger colony were more likely to produce and wean a litter than were those on the older colony. These two demographic characteristics of juveniles and yearlings appear consistent in rapidly growing prairie dog populations.

Simulated Effects of Different Shooting Strategies

In many of these studies, prairie dog populations appear to exhibit density-dependent growth; crowding with concomitant diminishing resources available to each individual leads to increased mortality (decreased survival), decreased reproduction, and/or increased emigration. An assumption of density-dependent population growth is that when a population approaches carrying capacity (K) the growth rate declines and eventually reaches R = 1.0 when N = K. The value of R at time t, R_t, depends on the population size N_t relative to K according to the equation, $R_t = R_{max}^{(1 - N_t/K)}$. When the population N_t is small, the exponent $(1 – N_t/K)$ is close to 1 and the population's growth rate R_t is close to the maximum possible, or R_{max}. As the population grows and approaches its carrying capacity, the growth rate R is much less than R_{max}, and when the population reaches carrying capacity, R = 1.0 because the exponent $(1 - N_t/K) = 0$.

If prairie dogs are viewed as an economic resource, the best strategy is to manage colonies for a sustained yield. A landowner or wildlife manager hoping to capitalize on prairie dog harvest might allow shooters to kill as many prairie dogs in a year as are produced. With density-dependent growth (R_{max} = 2.00, K = 1,000), a population growing from 20 to 1,000 animals produces the maximum number of animals (maximum yield) when it is approximately at half of carrying capacity (Peek, 1986). In this example, maximum yield = 209 when the population reaches 438 after 5 years of growth.

Harvesting the population at maximum productivity maximizes yield, but managing for maximum yield is difficult (Caughley and Sinclair, 1994). Removing animals from a population reduces the base population. The difficult task is determining what base population produces the best yield for the next year. If the harvest exceeds maximum yield and continues over time, the population will eventually decline to zero (Caughley and Sinclair, 1994).

Two common approaches to control harvest are (a) imposing a quota on numbers harvested and (b) regulating harvesting effort (Caughley and Sinclair, 1994). Regulating harvest by quotas is conceptually attractive: once the quota is attained, shooting stops. Determining when quotas for prairie dogs are reached might be problematic, however. If shooters consistently record prairie dogs killed and number of rounds fired, wildlife managers can estimate the number killed from the number of shots. Figure 1 demonstrates the problem with fixed annual harvest quotas. An initial population of 1,000 eventually stabilizes at 585 animals in 24 years if 195 prairie dogs are shot each year, but if the annual harvest exceeds 209 animals (the maximum yield when R_{max} = 2.00 and K = 1,000), then the population declines to extinction, doing so faster with larger harvests.

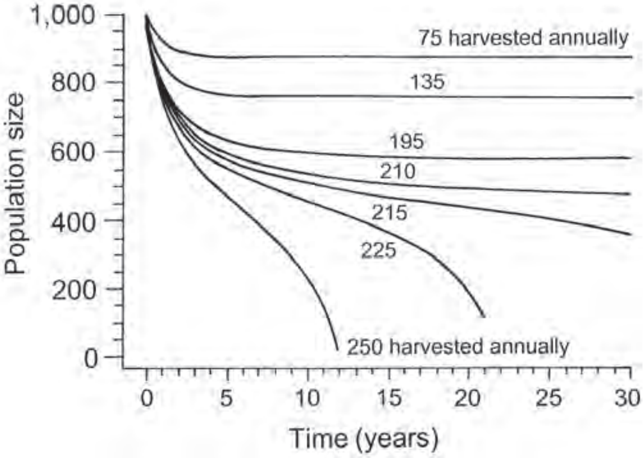

Figure 1. Effects of constant annual harvest quotas on a population with density-dependent growth (R_{max} = 2.00, K = 1,000) but no random variation in R_t. Annual harvest >209 animals (maximum yield) cannot be sustained, and the population eventually declines to zero.

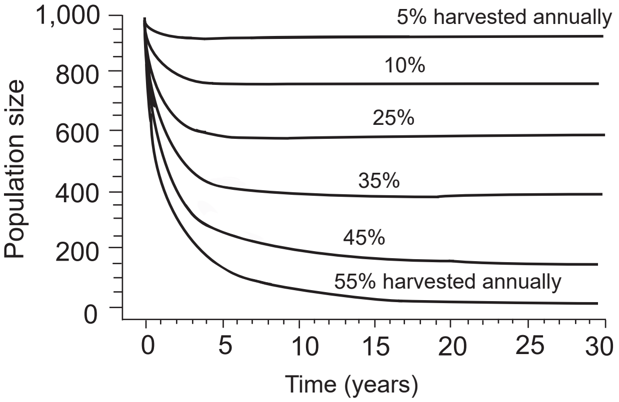

Figure 2. Deterministic predictions of a population with density-dependent growth (R_{max} = 2.00, K = 1,000) subject to different levels of proportional harvest annually.

Theoretically, controlling harvest effort removes some proportion of the population over time rather than a fixed number of animals each year. One way to control harvest effort is to limit the timing and duration of the harvest. Another way is to limit the number of shooters (Caughley and Sinclair, 1994). Figure 2 shows the outcome of various annual harvest levels as percentages of the current population. At an annual harvest rate of 25 percent, the population stabilizes at 585 animals, but in only 13 years, while the long-term average harvest (from t = 0 to t = 30) is approximately 199 animals.

To this point, population growth was assumed to be deterministic with no uncertainty in birth or death rates. Environmental variation from year to year, or day to day, and from one locale to another causes fluctuations in prairie dog populations' birth and death rates (Hoogland, 1995). In addition, individual animals in the same population have different reproductive capabilities or chances of survival. Recreational shooting of prairie dogs introduces additional uncertainty in population demographic parameters since age groups and sexes may be affected differently. Levels of variability might be measured at some point in time but cannot be predicted in the future. Stochastic population models provide for such uncertainty.

In the simulation examples provided so far, the finite rate of increase at time t, R_t, is equal to $R_{max}^{(1-Nt/K)}$. Annual variation in rates of birth, immigration, death, and emigration all contribute to variability of R_t. Annual variation in carrying capacity also causes variation in R_t. We introduce variation by increasing or decreasing the computed value of R_t by a random amount but within some defined limits, for example within ±20 percent of the computed value for R_t, which includes demographic variation as well as random variation in carrying capacity.

This simple approach was applied in 100 simulations to project population growth from an initial population of 20 animals with $R_{max} = 2.0$ and $K = 1{,}000$. The simulations show that the average population size stabilizes at approximately 1,000 animals (fig. 3) but, because of random variability of R_t, the population at $t = 15$ could range from 797 to 1,230 animals in any one simulation.

Random variation, now limited to only ±15 percent of the computed value for R_t, for example, is used to predict how an initial population of 1,000 ($N_0 = K$) with $R_{max} = 2.0$ responds to an annual quota of 195 animals harvested. The results (fig. 4) are different from those generated by the deterministic model (fig. 1). After 1,000 simulations, the stochastic model predicts a population of 406 (ranging from 0 to 819) at the end of 30 years with average annual harvest of 183. The model also predicts a 23 percent chance that the population will become extinct by $t = 30$. Risk of extinction increases with level of random variation in R_t. For example, with random variation ±10 percent of R_t, extinction within 30 years occurred in 1 percent of the trials, but a 46 percent chance of extinction is expected with random variation ±20 percent of R_t (after 1,000 simulations with an annual quota of 195).

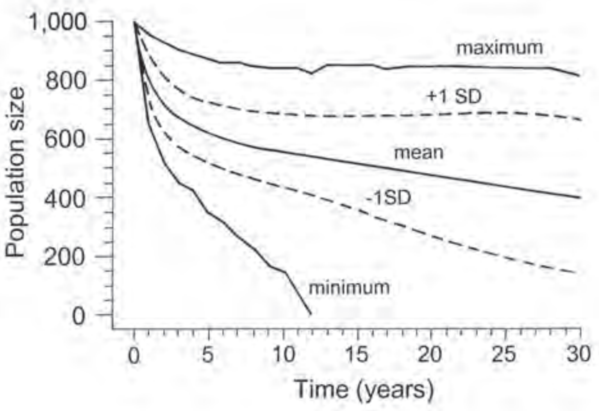

Figure 4. Results of 1,000 simulations with an annual harvest quota of 195 animals, an initial population of 1,000 animals, density-dependent population growth ($R_{max} = 2.00$), and random variation in the population growth rate each year (within ±15% of R_t after computation as $R_t = R_{max}^{(1-Nt/K)}$).

Alternatively, an annual harvest rate of 25 percent produces an expected population of 580 animals (ranging from 439 to 744 animals) after 30 years of simulation with average annual harvest of 197 animals but poses no risk of extinction (fig. 5), unlike the risk observed with fixed quota harvest (fig. 4). With demographic and environmental uncertainty, sustainable populations are more likely if harvested proportionally rather than by fixed quota. Implicit in modeling these two harvest strategies, however, is intensity of harvest management. Once set, the quota of 195 harvested did not change over time even though the population may have been declining

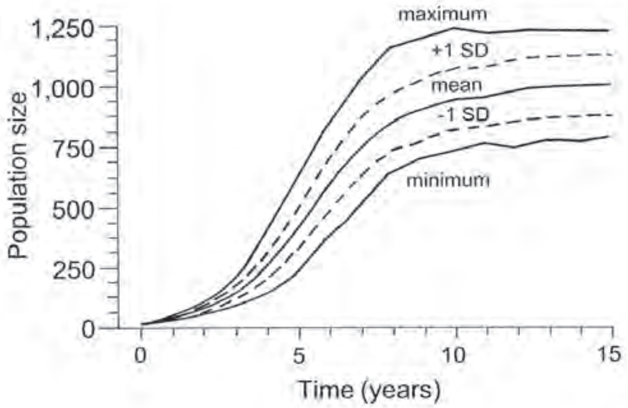

Figure 3. Results of 100 simulations of density-dependent population growth ($R_{max} = 2.00$, $K = 1{,}000$), but with random variation in the population growth rate each year (within ± 20% of R_t after computation as $R_t = R_{max}^{(1-Nt/K)}$).

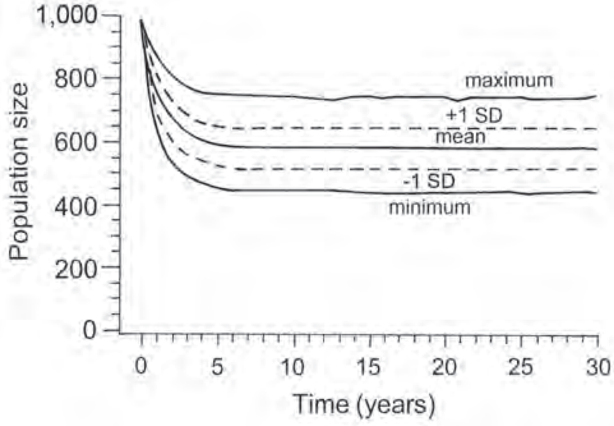

Figure 5. Results of 1,000 simulations with an annual harvest rate of 25%, an initial population of 1,000 animals, density-dependent population growth with $R_{max} = 2.00$, and random variation in the population growth rate each year (within ±15% of R_t after computation as $R_t = R_{max}^{(1-Nt/K)}$).

in a given simulation. Alternatively, numbers harvested were continuously adjusted when a harvest rate of 25 percent was applied. To ensure a sustainable population while realizing a desired annual harvest, the manager must monitor the dynamics of the target population and respond accordingly.

Proper application of either harvest strategy, whether by regulating harvest quota or by regulating harvesting effort, requires knowledge of the target population's carrying capacity and the species' R_{max}. Seldom are these parameters known with any certainty. A population at approximately K/2 is expected to yield the maximum number of animals that, in theory, could be harvested each year as a maximum sustained yield (MSY). Nevertheless, stochastic events in the environment and variability among individuals in a population can lead to substantial population fluctuations, and harvest should always be well below the estimated MSY (Caughley and Sinclair, 1994).

A third approach involves harvesting only when a population exceeds some threshold level, above which excess animals are taken (Lande and others, 1997). Threshold harvesting requires specific knowledge about population levels but produces high annual variation in harvest because populations below the threshold are not harvested (Lande and others, 1997). Threshold harvesting might be possible if a manager or landowner had never attempted to control prairie dogs and had monitored population levels under various environmental conditions so that average K could be estimated.

Recreational Shooting on Private Land for Prairie Dog Conservation

Of >660 livestock and agricultural operators surveyed in eastern Wyoming (Wyoming Agricultural Statistics Service, 2001), 23 percent expressed interest in a program of financial compensation for allowing prairie dogs on their land. The survey posed four types of management programs to respondents who expressed interest in financial compensation: (a) a shooting management program, (b) a cooperative shooter placement program to direct shooters to landowners willing to allow shooting, (c) a program to develop markets for prairie dogs as pets or for nature photography, and (d) a banking program in which other States would compensate Wyoming landowners for conserving prairie dogs (Wyoming Agricultural Statistics Service, 2001). Of these, prairie dog banking was the most popular (59 percent interested), a cooperative shooter placement program (57 percent interested) was second, followed by interest in shooting management (51 percent of respondents).

Respondents who expressed interest in programs with financial compensation considered \$74−\$86/ha annually to be reasonable (\$30−\$35/acre, median value). Generally, interest in maintaining or increasing the number of acres of prairie dog colonies on their land varied directly with the level of financial compensation. To attain \$74−\$86/ha in potential income from shooting, a landowner with 405 ha (1,000 acres) of prairie dog colonies, for example, could charge four shooters \$79−\$92 per person per day to shoot during the period between Memorial Day and Labor Day (approximately 95 days). Four shooters during that period are equivalent to 380 recreation days. Applying data from the Fort Belknap Indian Reservation (average of 38 prairie dogs shot per recreation day), the annual toll would be 14,440 prairie dogs killed, whereas 2,470 killed would be expected in a year at the rate of 6.5 prairie dogs per recreation day estimated in Colorado.

Densities of black-tailed prairie dogs in Conata Basin, S. Dak., range from 8/ha to 41/ha (Severson and Plumb, 1998). If that range of densities is applied to the simple example of a 405-ha colony on private land, then the population, estimated between 3,240 and 16,605 prairie dogs, could eventually be eliminated by recreational shooting under either the shooter success rate on Fort Belknap Indian Reservation or in Colorado. To ensure a future income, the private landowner would have to significantly decrease the number of recreation days spent shooting, which should concomitantly decrease the number of prairie dogs shot. In addition, to attain the desired income, the landowner would have to substantially increase fees charged per shooter.

Managing prairie dogs on private land for recreational shooting might be appropriate for some landowners and not others. Still, when faced with the apparent need or desire to control prairie dogs, opening land to shooters can provide landowners with an additional source of income and thus an incentive to support some level of occupied habitat that they otherwise would not tolerate.

Recreational Shooting on Black-footed Ferret Reintroduction Sites

Recreational shooting of prairie dogs has been totally or partially restricted on black-footed ferret (*Mustela nigripes*) reintroduction sites (Colorado Division of Wildlife and others, 2002), although there are few instances where effects of shooting closures on prairie dog populations have been monitored. In some instances, shooting closures coincided with changes in statewide prairie dog management practices following States' adoption of the Black-tailed Prairie Dog Conservation Assessment and Strategy and addendum (Luce, 2001). Closures to shooting have also been applied to other species of prairie dog, as in Arizona where black-footed ferrets were introduced in Gunnison's prairie dog colonies (B. Van Pelt, oral commun., 2003). In other cases, shooting closures were initiated to improve habitat for introduced black-footed ferrets and to ensure that ferrets, especially kits, would not be inadvertently shot (B. Perry, oral commun., 2003). Other wildlife, burrowing owls (*Athene cunicularia*) in particular, can be killed during recreational shooting of prairie dogs. Though not documented as a consequence of shooting prairie dogs, there are instances of substantial burrowing owl mortality by shooting (Haug and others, 1993; James and Espie, 1997).

In its review of a petition to list the black-tailed prairie dog under the Endangered Species Act, the U.S. Fish and Wildlife Service (1999) evaluated effects of recreational shooting, concluding in part that shooting may be a compensatory source of mortality in large populations with substantial reproduction. Where small prairie dog populations are depressed by other factors such as disease, shooting may be an additive source of mortality. Compensatory mortality, where one source of mortality offsets or replaces another source (Mackie and others, 1990), whether caused by harvest or predation, is most likely to occur in populations near their ecological equilibrium or carrying capacity (Peek, 1986; Bartmann and others, 1992; Boyce, 2000). In such density-dependent regulated populations, when density is high so are mortality rates, and a population decrease by whatever means results in higher survivorship in the remaining population, as long as removal of animals does not adversely affect reproduction the following year. When removal by harvest and/or predation is high enough to affect reproduction in subsequent years, mortality from those sources is likely to be additive and, if extreme, can force the target population to extinction.

By most accounts, ferret predation does not significantly depress prairie dog populations (Fagerstone, 1987) and would seem a source of compensatory mortality. Biggins and others (1993) estimated annual consumption of 109 prairie dogs by one black-footed ferret family group (1 adult female, 3.3 young, and 0.5 adult male) while recognizing the potential for substantial prairie dog predation by other species. Assuming moderate levels of mortality by other sources, Biggins and others (1993) estimated that a stable population of 763 prairie dogs would sustain a ferret family group for 1 year. Using an age-dependent predation model of ferrets and prairie dogs, Klebanoff and others (1991) concluded that as many as 2,000 prairie dogs per ferret may be necessary to sustain a stable predator-prey system. A stable system can also be attained with fewer prairie dogs—though not as few as 763—but only if prairie dog survivorship or fecundity rates increase (Klebanoff and others, 1991). We are not aware if either estimation approach has been field tested.

Prairie dog mortality by unregulated recreational shooters can vastly exceed predation by black-footed ferrets, thus affecting prairie dog survivorship and potentially affecting fecundity and recruitment. Recreational shooting can be additive mortality, potentially more so on black-tailed prairie dog colonies than on Gunnison's or white-tailed colonies (table 2). Management agencies have recognized that, even with closures of specific areas, recreational shooting has continued and that enforcement of shooting closures is problematic (V. Kopcso, oral commun., 2003). Until more is known about effects of recreational shooting on prairie dogs that are the primary prey resource for black-footed ferrets, managers are wise to restrict shooting and enforce closures, particularly on ferret reintroduction sites inhabited by black-tailed prairie dogs.

References Cited

Akçakaya, H.R., Burgman, M.A., and Ginzburg, L.R., 1999, Applied population ecology principles and computer exercises using RAMAS® EcoLab 2.0: Sunderland, Mass., Sinauer Associates, Inc., 285 p.

Bartmann, R.M., White, G.C., and Carpenter, L.H., 1992, Compensatory mortality in a Colorado mule deer population: Wildlife Monographs, v. 121, p. 1–39.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Boyce, M.S., 2000, Modeling predator-prey dynamics, *in* Boitani, L., and Fuller, T.K., eds., Research techniques in animal ecology—controversies and consequences: New York, Columbia University Press, p. 253–287.

Caughley, G., and Sinclair, A.R.E., 1994, Wildlife ecology and management: Cambridge, Mass., Blackwell Science, 334 p.

Colorado Division of Wildlife, 2002, 1998/99 small game harvest survey statistics: http://wildlife.state.co.us/hunt/small_game/89_99smgamesurveystats1.htm.

Colorado Division of Wildlife, 2003, 2002/03 small game harvest report: http://wildlife.state.co.us/hunt/small_game/harvest_statistics_02-03/small_game_harvest.pdf.

Colorado Division of Wildlife, Bureau of Land Management, and U.S. Fish and Wildlife Service, 2002, Prairie dog shooting and black-footed ferret recovery in northwest Colorado: Grand Junction, Colo., U.S. Fish and Wildlife Service, 13 p.

Cully, J.R., Jr., 1997, Growth and life-history changes in Gunnison's prairie dogs after a plague epizootic: Journal of Mammalogy, v. 78, p. 146–157.

Fagerstone, K.A., 1987, Black-footed ferret, long-tailed weasel, short-tailed weasel, and least weasel, *in* Novak, M., Baker, J.A., Obbard, M.E., and Malock, B., eds., Wild furbearer management and conservation in North America: Ontario, Canada, Ministry of Natural Resources, p. 548–573.

Fitzgerald, J.P., Meaney, C.A., and Armstrong, D.M., 1994, Mammals of Colorado: Niwot, Denver Museum of Natural History and University Press of Colorado, 467 p.

Garrett, M.G., and Franklin, W.L., 1988, Behavioral ecology of dispersal in the black-tailed prairie dog: Journal of Mammalogy, v. 69, p. 236–250.

Garrett, M.G., Hoogland, J.L., and Franklin, W.L., 1982, Demographic differences between an old and a new colony of black-tailed prairie dogs (*Cynomys ludovicianus*): American Midland Naturalist, v. 108, p. 51–59.

Gigliotti, L., 2001, Prairie dog shooting in South Dakota: Pierre, South Dakota Department of Game, Fish and Parks, 35 p.

Haug, E.A., Millsap, B.A., and Matell, M.S., 1993, Burrowing owl (*Speotyto cunicularia*), *in* Poole, A., and Gill, F., eds., The birds of North America: Washington, D.C., American Ornithologists' Union, and Philadelphia, Pa., Academy of Natural Sciences, no. 61, p. 1–20.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing mammal: Chicago, University of Chicago Press, 557 p.

James, P.C., and Espie, R.H.M., 1997, Current status of the burrowing owl in North America—an agency survey, *in* Liner, J.L., and Steenhof, K., eds., The burrowing owl, its biology and management—including the Proceedings of the First International Symposium: Raptor Research Report, no. 9, p. 3–5.

Keffer, K., Gordon, K., and Anderson, S., 2000, Effects of recreational shooting on behavior of black-tailed prairie dogs: Laramie, University of Wyoming, Cooperative Fish and Wildlife Research Unit, 15 p.

Klebanoff, A., Minta, S., Hastings, A., and Clark, T.W., 1991, Age-dependent predation model of black-footed ferrets and prairie dogs: SIAM Journal of Applied Mathematics, v. 51, p. 1053–1073.

Knowles, C.J., 1986, Population recovery of black-tailed prairie dogs following control with zinc phosphide: Journal of Range Management, v. 39, p. 249–251.

Knowles, C.J., 1988, An evaluation of shooting and habitat alteration for control of black-tailed prairie dogs, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 53–56.

Koford, C.B., 1958, Prairie dogs, whitefaces, and blue grama: Wildlife Monographs, v. 3, p. 1–78.

Lande, R., Saether, B., and Engen, S., 1997, Threshold harvesting for sustainability of fluctuating resources: Ecology, v. 78, p. 1341–1350.

Lower Brule Sioux Tribe, 2002, Black-tailed prairie dog management plan: Lower Brule, S. Dak., Lower Brule Sioux Department of Wildlife, Fish, and Recreation, 18 p.

Luce, B., ed., 2001, Addendum—an umbrella, multi-state approach for the conservation and management of the black-tailed prairie dog, *Cynomys ludovicianus*, in the United States: Cheyenne, Wyo., Black-tailed Prairie Dog Conservation Team, 22 p.

Mackie, R.J., Hamlin, K.L., Pac, D.F., Dusek, G.L., and Wood, A.K., 1990, Compensation in free-ranging deer populations: Transactions of the North American Wildlife and Natural Resources Conference, v. 55, p. 518–526.

Nebraska Game and Parks Commission, 2001, Nebraska conservation plan for the black-tailed prairie dog: Lincoln, Nebraska Game and Parks Commission, draft report, July 2001, http://www.ngpc.state.ne.us/wildlife/pdogplan.html.

North Dakota Game and Fish Department, 2001, Black-tailed prairie dog state management plan: Bismarck, North Dakota Game and Fish Department, 14 p.

Peek, J.M., 1986, A review of wildlife management: Englewood Cliffs, N.J., Prentice-Hall, 486 p.

Radcliffe, M.C., 1992, Repopulation of black-tailed prairie dog (*Cynomys ludovicianus*) colonies after artificial reduction: Frostburg, Md., Frostburg State University, M.S. thesis, 30 p.

Severson, K.E., and Plumb, G.E., 1998, Comparison of methods to estimate population densities of black-tailed prairie dogs: Wildlife Society Bulletin, v. 26, p. 859–866.

Smith, R.E., 1967, Natural history of the prairie dog in Kansas: Lawrence, University of Kansas, Museum of Natural History and State Biological Survey of Kansas, 39 p.

South Dakota Prairie Dog Work Group, 2001, South Dakota black-tailed prairie dog management plan: Pierre, South Dakota Department of Game, Fish and Parks, draft report 2—October 2001, 74 p., http://www.sdgf.info/Publications/pdmplan.pdf.

Stockrahm, D.M.B., and Seabloom, R.W., 1988, Comparative reproductive performance of black-tailed prairie dog populations in North Dakota: Journal of Mammalogy, v. 69, p. 160–164.

Tileston, J.V., and Lechleitner, R.R., 1966, Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado: American Midland Naturalist, v. 75, p. 292–316.

U.S. Fish and Wildlife Service, 1999, Positive 90-day finding for a petition to list the black-tailed prairie dog: Denver, Colo., U.S. Fish and Wildlife Service, Region 6, 50 p.

Vosburgh, T., 2000, Impacts of recreational shooting on prairie dogs on Fort Belknap Reservation, Montana, *in* Vosburgh, T., and Stoneberg, R., eds., 1999 annual report of black-footed ferret recovery activities: Fort Belknap Reservation, Mont., 4 p.

Vosburgh, T.C., and Irby, L.R., 1998, Effects of recreational shooting on prairie dog colonies: Journal of Wildlife Management, v. 62, p. 363–372.

Wyoming Agricultural Statistics Service, 2001, Black-tailed prairie dog management survey, report of results: Cheyenne, Wyoming Department of Agriculture, 21 p.

Habitat Preferences and Intraspecific Competition in Black-footed Ferrets

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Abstract

We used radio-telemetry data (28,560 positional fixes) collected on 153 black-footed ferrets (*Mustela nigripes*) to (1) reexamine the assumed obligate relationship of these ferrets to prairie dogs (*Cynomys* spp.), (2) investigate habitat preferences of ferrets at a small scale (<1 ha), and (3) gain insight into competition among ferrets for habitat patches of varying quality. We used densities of prairie dog burrows as an indicator of habitat quality because burrows are presumably valuable to ferrets as cover and because density of burrows is correlated to density of prairie dogs. Burrow density summaries were generated from maps of all burrows on ferret reintroduction sites in Montana and South Dakota. Aboveground movements by ferrets were mostly (89 percent) within the boundaries of prairie dog colonies or associated with circuits involving return to a colony (10 percent), with no evidence that ferrets sought to occupy alternative habitats. Sampling with 0.07-ha plots suggested that dispersion of prairie dog burrows within colonies was neither uniform nor random. Burrows were clumped, and ferrets preferred ($P < 0.001$) patches of habitat with high densities of burrows compared to samples taken at random points on the colonies they occupied. The magnitude of preference (the difference between use and availability) was greatest for resident young ferrets compared to their recently released counterparts, whether the newcomers were compared with residents of 2–4 weeks ($P = 0.039$) or >1 year ($P = 0.048$). Also, preference was stronger for wild-born young ferrets than for young captive-born ferrets released to augment the wild population ($P = 0.040$). This additional evidence for competition among ferrets, and for an advantage of prior residency, raises conservation concerns. The energetics-based model commonly used to predict ferret densities at reintroduction sites does not consider competition, which likely leads to overestimation of the densities of ferrets attainable in high-quality habitat. During sequential releases of ferrets, prior residency may handicap success of newcomers, even though the latter may have higher potential fitness. Although the manner of initial colonization of available habitat by black-footed ferrets, and their subsequent competition for it, was suggestive of an ideal despotic distribution, we did not assess effects of prey density or burrow density on fitness.

Keywords: black-footed ferret, competition, *Cynomys*, endangered species, habitat, ideal despotic distribution, ideal free distribution, *Mustela nigripes*, prairie dog, prior residency

Introduction

Conservation efforts for the highly endangered black-footed ferret (*Mustela nigripes*) include a captive breeding program that rescued the species from a remnant population of 10 animals in Wyoming (fig. 1) during the winter of 1985–86. That captive breeding program currently produces annual surpluses of 200–300 kits for reintroduction (Marinari and Kreeger, this volume). Ferrets have been reintroduced at sites in six U.S. States and Chihuahua, Mexico (Lockhart and others, this volume). Releases of ferrets into unoccupied and occupied habitat, and monitoring of wild-born ferrets, provided unique opportunities to evaluate large-scale habitat

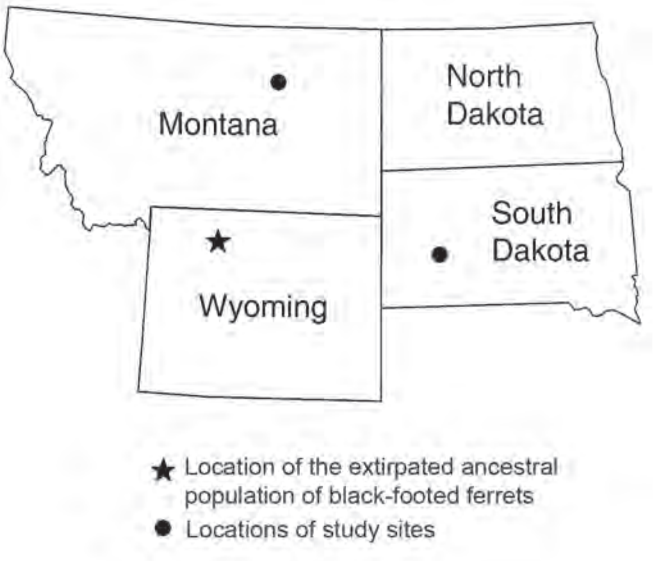

Figure 1. The site near Meeteetse, Wyo., that provided ancestral stock for the captive breeding program, and study sites in Montana and South Dakota where black-footed ferrets (*Mustela nigripes*) were released.

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use by ferrets (objective 1), habitat preferences at small scales (objective 2), and relationships between ferret territoriality and habitat quality (objective 3), all of which are relevant to ferret conservation.

Considerable evidence supports a strong relationship between prairie dogs (*Cynomys* spp.) and black-footed ferrets. A summary by Anderson and others (1986) indicates that almost all recent ferret specimens were collected from areas within the composite ranges of black-tailed prairie dogs (*C. ludovicianus*), white-tailed prairie dogs (*C. leucurus*), or Gunnison's prairie dogs (*C. gunnisoni*), and most of the explicit descriptions of locality, where provided, mentioned prairie dog colonies. The last extant ferret populations were found on prairie dog colonies, and studies of those ferrets revealed intensive use of prairie dog colonies (Hillman and others, 1979; Biggins and others, 1985). Prairie dogs are the predominant prey taken by black-footed ferrets (Sheets and others, 1972; Campbell and others, 1987). Strategies for evaluating black-footed ferret habitat (Linder and others, 1972; Forrest and others, 1985; Flath and Clark, 1986; Houston and others, 1986; Biggins and others, 1993) universally assumed that prairie dog colonies were a primary requirement. Others, however, have questioned the characterization of black-footed ferrets as extremely specialized (Owen and others, 2000). One objective of this study was to further document the use of habitats by ferrets on a large scale, using data from radio tracking and maps of black-tailed prairie dog colonies in Montana and South Dakota, to reexamine the degree of dependence of black-footed ferrets on prairie dogs.

Evaluations of ferret habitat are mostly large scale, conducted on colonies hundreds of hectares in size and on complexes occupying thousands of hectares, leaving the details of how ferrets use their local environments largely unexplored. If black-footed ferrets are obligate predators on prairie dogs and variation exists in densities of prairie dogs and their burrows within their colonies, we predict that intensity of ferret activity will correlate positively with density of prairie dogs when habitat is examined at scales smaller than colonies. Thus, our second objective was to evaluate preferences of ferrets by using sample parcels of land <1 ha in size. To address small-scale habitat preferences and the following objective, we used burrow densities as an indicator of habitat quality. Prairie dog burrow densities should give a suitable measure of habitat quality for black-footed ferrets, in part because they correlate to density of the prairie dog prey (Biggins and others, 1993) and in part because burrows have intrinsic value to ferrets as refuges from predators and adverse weather and as dens to rear young.

Black-footed ferrets, like many other mustelids, appear to be intrasexually territorial (Powell, 1979; Miller and others, 1996). In typical carnivore fashion, females attempt to control access to food resources, while males attempt to control access to females (Ewer, 1973). Although several factors in varying combinations appear to contribute to an organism's resource holding power (e.g., relative size of contestants, age, experience in former contests), prior residency often confers significant advantages. The residency advantage is widespread among several taxa, including insects (Davies, 1978), arachnids (Riechert, 1978), decapods (Jennions and Backwell, 1996), fish (Harwood and others, 2003), amphibians (Mathis and others, 2000), and mammals (Neumann, 1999). Because many of the ferrets we studied were released into unfamiliar terrain that was either unoccupied by ferrets or occupied by ferrets for known periods of time, it was possible to examine the effect of prior residency.

Release of ferrets into vacant habitat allowed us to assess the sequence of occupancy. If habitat patches are heterogeneous, the order in which they become colonized or abandoned should relate to quality of those patches as perceived by occupants (Wiens, 1976; Krohn, 1992). Ideal free distribution theory predicts such an interrelationship between population density and carrying capacity of patches in heterogeneous habitats (Fretwell and Lucas, 1970). If order of occupancy reflects quality of habitat patches, then assessment of the colonization process also may lead to improved understanding of source-sink dynamics after habitats become fully populated (Howe and others, 1991; Pulliam and Danielson, 1991). To evaluate intraspecific competition for habitat and order of occupancy of habitat patches, we again utilized radio-telemetry data, overlaying ferret locations onto digitized maps of prairie dog burrows within the colonies studied.

Methods

We radio tracked 153 black-footed ferrets on prairie dog colonies at UL Bend National Wildlife Refuge, Mont., and on the Buffalo Gap National Grassland, S. Dak., during September–November 1994–97 (figs. 1 and 2). Some of the resulting 28,560 telemetric fixes were used for multiple studies; the UL Bend data from 1994 and 1995, for example, were also used in the comparisons of adults and kits reported herein (Biggins, Godbey, Livieri, and others, this volume). We affixed transmitters having 20-cm whip antennas to wool collars of 1-cm width, using Teflon® (DuPont, Wilmington, Del.) heat-shrink tubing (Biggins and others, 1999; Biggins, Godbey, Miller, and Hanebury, this volume). We weighed and radio collared ferrets that were wild caught or captive bred (while the animals were held under isoflurane anesthesia) and inserted passive integrated transponder chips for long-term identification (Biggins, Godbey, Matchett, and others, this volume). Ferrets from captive breeding facilities were reared under a variety of strategies and released during August–November with no more than 1-day acclimation in onsite cages (Biggins and others, 1998).

We radio tracked ferrets from fixed stations fitted with dual-beam, 11-element Yagi antennas on 6-m masts and used null-peak direction finding and triangulation to fix each ferret's position at intervals of 7–60 minutes while the animals

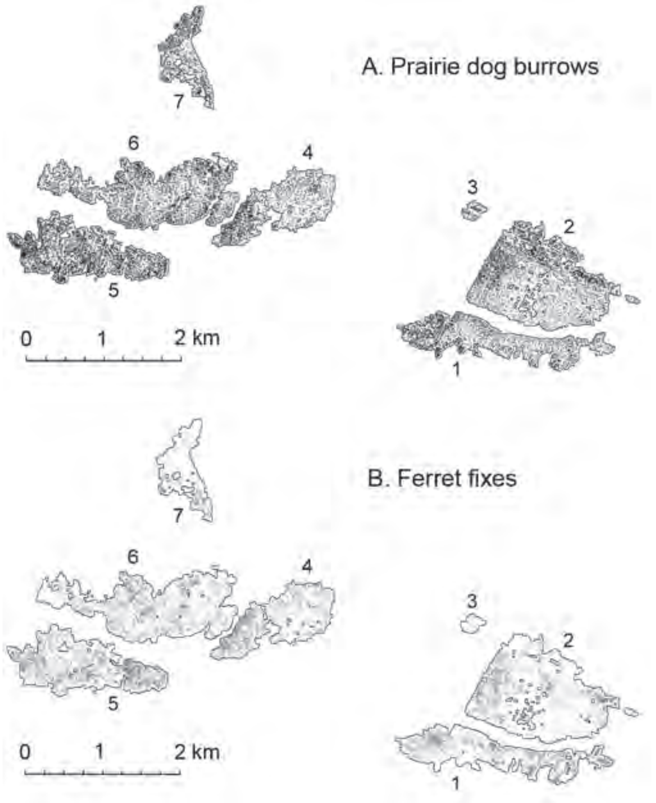

Figure 2. Distribution of black-tailed prairie dog (*Cynomys ludovicianus*) burrows (A) and black-footed ferret (*Mustela nigripes*) telemetric fixes (B) on colonies at UL Bend National Wildlife Refuge, Mont. Each dot is a burrow opening or telemetric fix; density of resulting stippling thus reflects density of burrows or fixes. Attributes for numbered colonies are summarized in table 1.

were active above ground (Biggins and others, 1999; Biggins, Godbey, Livieri, and others, this volume). We developed station-specific error estimates from test data by using differences between telemetry-derived azimuths and azimuths to transmitters of known location (Biggins and others, 1999; Biggins, Godbey, Miller, and Hanebury, this volume). Aboveground activity of black-footed ferrets is mostly nocturnal (Biggins and others, 1986; Biggins, 2000), so we limited monitoring of ferrets to hours of darkness for 2 weeks to 2 months postrelease. We recorded estimated locations of ferrets and associated error polygons as Universal Transverse Mercator coordinates derived from paired azimuths with program TRITEL (Biggins, Godbey, Miller, and Hanebury, this volume).

We recorded locations of prairie dog burrow openings (henceforth, such openings will be referred to as burrows) with Global Positioning System (GPS) receivers, differentially corrected to provide point estimates with errors of <1 m. ArcInfo® Version 8.2 (Environmental Systems Research Institute, Inc., Redlands, Calif.) was used for all vector processing, and the GRID module was used for all raster modeling. The vector point data for all prairie dog burrows and ferret locations in the study were consolidated into the Universal Transverse Mercator Zone 13 projection using the North American Datum of 1927. The GRID module was used to convert the vector points to 1-m^2 cells. To create a map of each prairie dog colony, cells were expanded by 10 m in every direction. Thus, the maps of colonies (fig. 2A,B; table 1) can be envisioned to include a buffer of 10 m beyond the outermost burrows and to exclude spaces within the outer boundary that are >10 m from the nearest burrow.

Use of Habitats Other than Prairie Dog Colonies

To investigate the broad-scale preference of black-footed ferrets for prairie dog colonies, we examined ferret use of the colonies as defined above and their use of noncolony areas. Ferret fixes were classified as being on or off colonies. Because there were nearby colonies in the South Dakota complex that were not mapped with the system described, ferret fixes that were not on mapped colonies could have been on other colonies. Thus, we did not use South Dakota data for these large-scale assessments. Similarly, a subset of ferrets in Montana (14 animals living near the eastern boundary of the subcomplex) had access to colonies that were not mapped with this system and were likewise eliminated from the analysis. The remaining data used for this overview included 24,512 fixes on 108 radio-tagged animals, including released and resident adults and kits. Because ferrets presumably must make exploratory moves to assess the distribution of prairie dogs, and because some ferrets traversed noncolony areas during routine travels between colonies, fixes that were off colonies do not necessarily imply that ferrets were actually living in areas not occupied by prairie dogs. We estimated the relative use of noncolony areas attributable to these phenomena, defining an off-colony excursion as a movement involving ≥2 fixes

Table 1. Black-tailed prairie dog (*Cynomys ludovicianus*) colonies where prairie dog burrows were mapped. Numbers for Montana colonies correspond to the numbered colonies of figure 2.

Colony	Area (ha)	Burrows/ha
Montana		
1. South Locke	90.1	57.9
2. North Locke	166.0	48.9
3. Small	5.0	64.1
4. Sagebrush	79.8	49.8
5. South Hawley	102.4	79.4
6. North Hawley	144.0	54.6
7. Wilderness	42.2	62.1
South Dakota		
North Sage Creek	160.1	138.9

away from a colony, followed by return to a colony. We also tallied the number of fixes associated with intercolony moves and dispersal moves (movement with no return to a colony).

Preferences Within Prairie Dog Colonies

We examined habitat preferences of ferrets within colonies at a small scale by comparing counts of the number of mapped burrows in circular plots of 0.07 ha (radius = 15 m) surrounding ferret fixes with counts in similar plots surrounding random points on colonies (fig. 3), sampling with replacement (plots were allowed to overlap). To be included in the analysis, the boundary of a sample plot was required to be entirely within a colony as defined above. Ferrets with ≤3 fixes were excluded. To characterize densities of prairie dog burrows on the Montana colonies, we sampled 20,328 plots at random points and compared those to plots centered on 21,185 fixes for 110 ferrets. In South Dakota, we counted burrows within plots surrounding 427 fixes (for 19 ferrets) and 465 random points. Because many ferret fixes for individual animals were serially autocorrelated (e.g., the sequential fixes of fig. 3), we summarized density of burrows within plots as mean densities for each animal and used those means in all subsequent analyses. Thus, sample sizes became numbers of animals (not numbers of fixes). We further restricted this data set to include only those ferrets radio tracked >3 days; estimates for animals radio tracked for shorter periods were deemed unreliable.

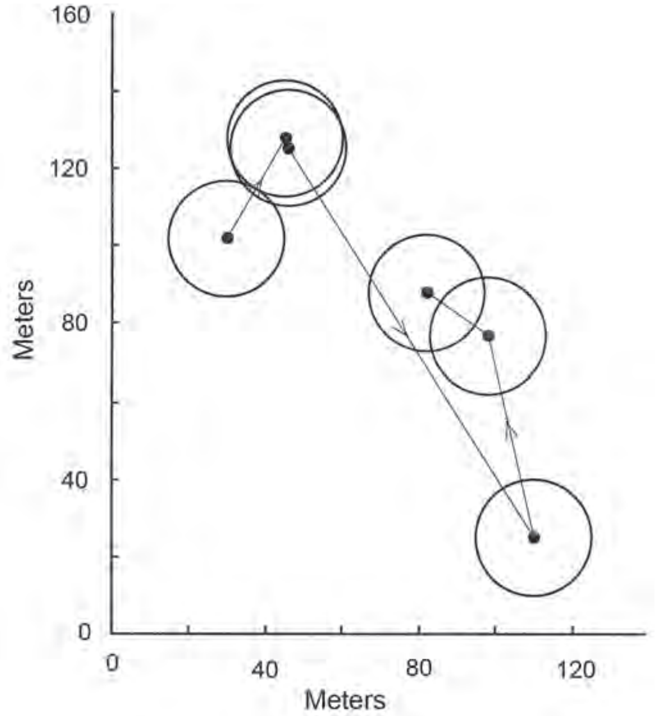

Figure 3. Example of encircling a series of telemetric fixes with plots of 15-m radius, within which black-tailed prairie dog (*Cynomys ludovicianus*) burrow entrances were counted, for black-footed ferret (*Mustela nigripes*) no. 32, North Sage Creek, S. Dak., on the night of October 26–27, 1997. Overlapping plots were allowed for both ferret fixes and random points (sampling with replacement).

A patchy distribution of habitat (burrows) within prairie dog colonies is a prerequisite for allowing choice by ferrets. Frequencies of counts within the plots described above would be expected to follow a Poisson distribution if dispersion of burrow openings on colonies were random (Ricklefs, 1990). For a Poisson distribution, the variance in counts is equal to the mean; evenly spaced burrow openings will produce a variance less than the mean, and clumped burrow openings will result in variance greater than the mean. We examined the variance:mean ratios for the counts within our samples of circular plots to provide an indication of dispersion of burrow openings in each colony.

Intraspecific Competition for Habitat

To assess intraspecific competition for habitat, we compared habitats occupied by groups of black-footed ferrets that were expected to differ in competitive standing. We predicted that (1) resident adult ferrets would have a competitive advantage over their wild-born kits, (2) wild-born kits would have an advantage compared to released kits, (3) kits released first would be more competitive than kits released subsequently into the same area in the same year, (4) larger kits would have an advantage over smaller kits, and (5) kits released into unoccupied habitat during the first year of reintroductions at a site would have an advantage over kits released in subsequent years to augment a population. As outlined above, we assumed burrow density correlated positively with habitat quality. We thus expected dominant ferrets to occupy areas of higher burrow density compared to their less competitive counterparts. We assessed burrow densities estimated from the sample of 0.07-ha plots described above.

As implied by the groups in comparisons 1–5 above, various overlapping subsets of animals were used for analyses. Montana data were best suited for this assessment because ferrets were released in multiple years on several colonies, they were released in several consecutive groups in the same colonies during 2 years, and resident ferrets were monitored during 1 year. As with the broader analysis above, we included only those ferrets radio tracked >3 days. Within the Montana data set, the comparison of adult and young resident ferrets (1 above) was limited to the 1997 subset of data collected on Hawley and associated colonies, as was the comparison of wild-born and released young ferrets (2). We compared groups of young ferrets released sequentially during the same years at the same sites (3) within the 1994 and 1995 data sets at all colonies. Measures of mass (4) were available for Montana animals released in 1994 and 1995, and that variable was included in the assessment of within-year sequential releases. Because sexes are dimorphic, we included sex in the model to interact with mass. Finally, we compared young ferrets released into vacant habitat at Hawley and associated colonies in 1995 with young ferrets released into that habitat in 1997, when portions of it were occupied by resident ferrets (5 above). That 368.3-ha area of prairie dog colonies (the four western colonies of fig. 2A,B) was occupied by at least 8 adults and 19 kits that we marked (not all were monitored via the radio tracking of this study).

To provide additional evidence on the effect of competition, we assessed numbers of released ferrets that moved between colonies in 1995, when these ferrets were released into habitat without a resident population of ferrets, and in 1997, when ferrets were released into the same prairie dog colonies to augment an existing population.

Statistical Evaluation

For statistical comparisons, we reduced burrow density data to animal-specific estimates for habitat they used, paired with colony-specific estimates for colonies they occupied. If an animal occupied more than one colony, we calculated separate pairs of estimates (use and availability) for each colony. We used multivariate general linear modeling (repeated measures) to evaluate differences between burrow densities for colonies and for habitat used by ferrets, assuming that all habitat on the colony occupied by a ferret was potentially available to that ferret. General models were reduced to more parsimonious versions by backward elimination using partial *F*-tests, when appropriate. Comparisons were judged as significant if the probability of committing a Type I error was ≤0.05. Exact chi-square analyses (Berry and Mielke, 1985) assisted in evaluation of proportions of ferrets engaging in intercolony movements.

Results

Use of Habitats Other than Prairie Dog Colonies

Of the 24,512 total fixes used, 2,744 (11.19 percent) were off colonies. There were 88 instances of intercolony movement. Some of the off-colony locations were solitary telemetric fixes that could be the result of radio-tracking error. Because clusters of sequential fixes provide information on pattern of movement, we assessed off-colony moves using groups of ≥2 consecutive fixes away from a colony. The number of clustered fixes off colonies was 2,010 in 474 bouts of movement made by 87 animals with 1 to 24 bouts per ferret; 1,767 of these (87.91 percent) were associated with exploratory excursions involving returns to the colony of origin (fig. 4) and intercolony moves (fig. 5). If these cluster-based estimates are applied to the total of 11.19 percent of fixes away from prairie dog colonies, it appears that only about 1.4 percent (0.1119 * 0.1209 = 0.0135) of the total number of off-colony fixes may involve dispersal (fig. 6) without known return to the colony of origin or travel to another colony.

Preferences Within Prairie Dog Colonies

Patchiness in dispersion of burrow openings was highly evident, as indicated by variance:mean ratios >>1.0 for all colonies (fig. 7) sampled by 0.07-ha circular plots. Overall, black-footed ferrets preferred patches of habitat with densities of prairie dog burrows higher than the averages for colonies they occupied (fig. 8). Our general statistical model evaluated overall differences between ferret plots and random plots (hereafter referred to as preference) and the effects of sex and colony. Sex accounted for relatively little variation ($F_{1,149}$ = 0.130, P = 0.719) and was removed from the model. Preference of sites with elevated densities of burrows was consistent ($F_{1,154}$ = 16.996, P < 0.001) among colonies (fig. 8), but the magnitude of the differences between burrow densities in

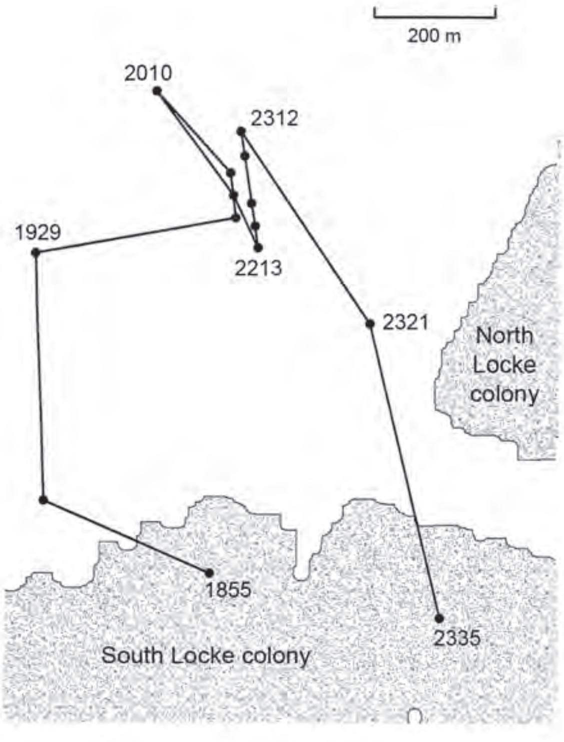

Figure 4. An example of an exploratory excursion away from a black-tailed prairie dog (*Cynomys ludovicianus*) colony by young male black-footed ferret (*Mustela nigripes*) no. 24, UL Bend National Wildlife Refuge, Mont., October 20, 1994. Numbers associated with points are times of day.

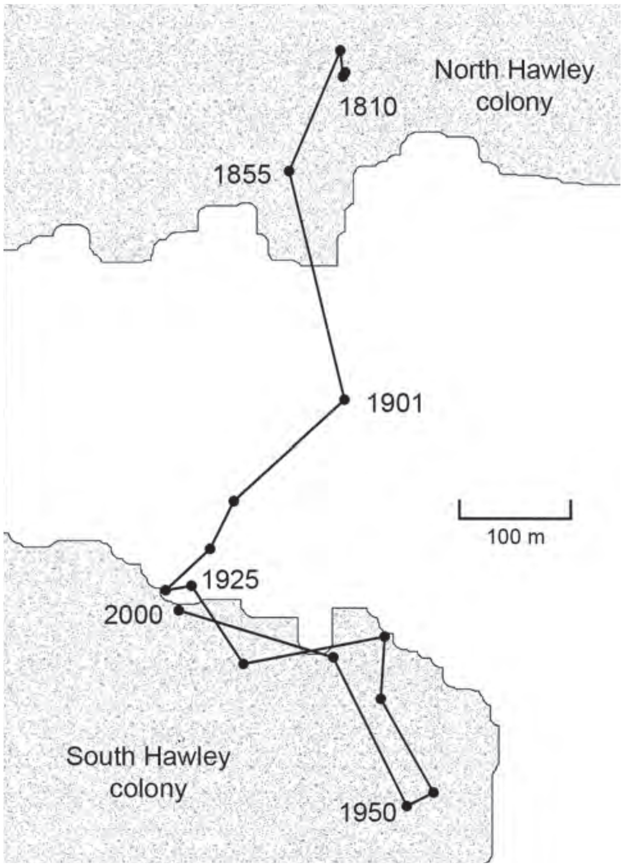

Figure 5. An example of an intercolony move by young female black-footed ferret (*Mustela nigripes*) no. 71, UL Bend National Wildlife Refuge, Mont., November 5, 1995. Numbers associated with points are times of day.

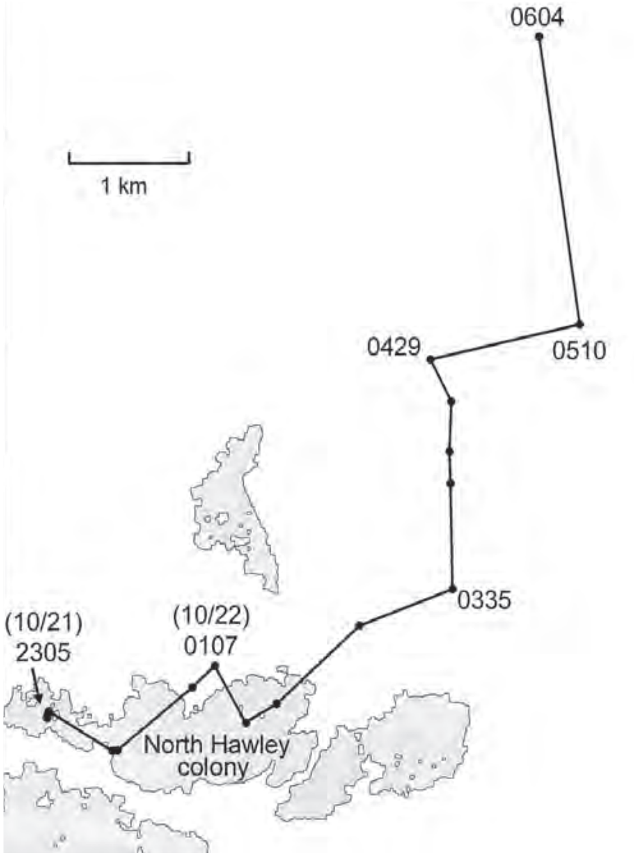

Figure 6. An example of dispersal away from black-tailed prairie dog (*Cynomys ludovicianus*) colonies by young male black-footed ferret (*Mustela nigripes*) no. 213, October 21–22, 1997. Numbers associated with points are times of day.

ferret and random plots appeared to vary (preference × colony interaction; $F_{7,154} = 2.144$, $P = 0.042$).

Intraspecific Competition for Habitat

Three of the four general models in these analyses had only class of animal in the repeated measures comparison of random and ferret-centered estimates of burrow density; these three models were not further reduced. Failure of sex and mass (in the 1994 and 1995 Montana data) to explain significant variation ($P > 0.160$) resulted in reduction of that model to a simpler submodel resembling the others used to evaluate competition. Each of these subsets of data reflected the significant habitat preferences of ferrets ($P \leq 0.010$) that were documented in the more general treatment above. Our primary focus in evaluations of competition was centered on the interaction term of each model that tested whether classes of ferrets influenced variation in differences between habitat used and habitat available (preference). In that regard, only the comparison between habitat preferences of resident adult ferrets and their resident young failed to explain significant variation (preference × age interaction; $F_{1,31} = 0.579$, $P = 0.452$). As predicted, wild-born resident young ferrets were

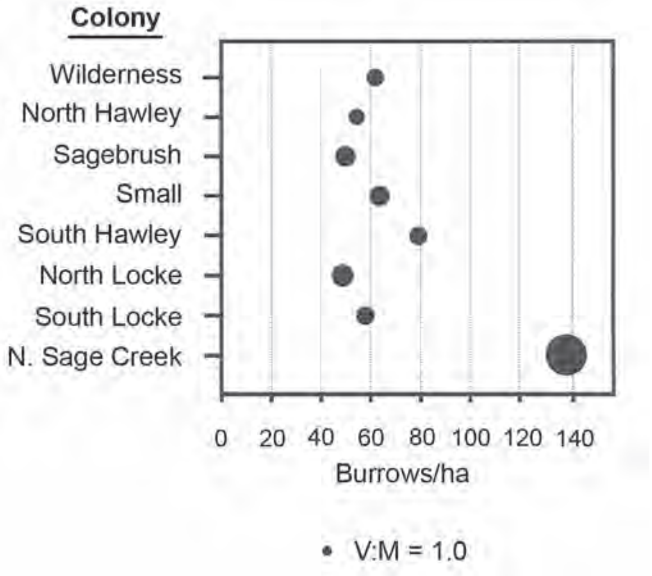

Figure 7. Densities of burrows on study colonies and variance to mean ratios (V:M) estimated from samples of 0.07-ha plots. Diameter of symbol is proportionate to V:M ratio within sample of plots.

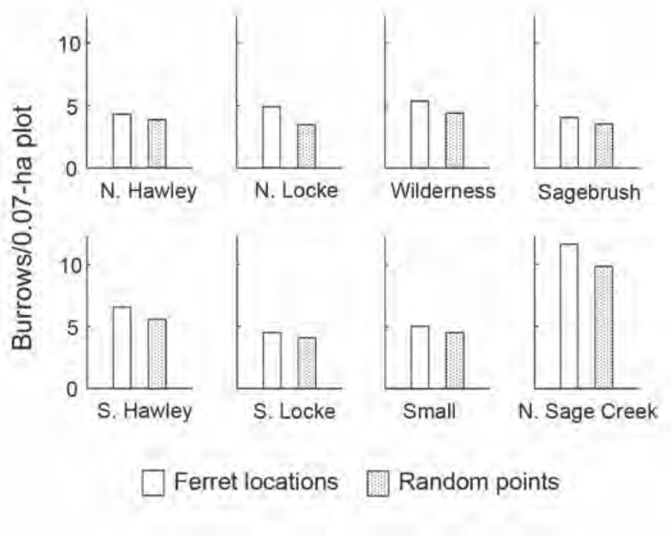

Figure 8. Burrow densities within plots encircling telemetric fixes of black-footed ferrets (*Mustela nigripes*) and within plots at random points on black-tailed prairie dog (*Cynomys ludovicianus*) colonies.

able to exercise a higher level of preference than did released young (fig. 9) (preference × origin interaction; $F_{1,51}$ = 4.445, P = 0.040), first-released young ferrets were more selective than were young released later the same year (fig. 10) (preference × sequence interaction; $F_{1,67}$ = 4.430, P = 0.039), and young ferrets released into vacant habitat were more selective than were young used to augment the population in that habitat during a later year (fig. 11) (preference × year interaction; $F_{1,62}$ = 4.063, P = 0.048).

Most (12/13 = 92.3 percent) young ferrets added to the resident population in the western colonies of the UL Bend complex in 1997 moved between colonies. That proportion was significantly different (X^2 = 13.789, df = 1, P < 0.001) from the corresponding proportion for 1995 (8/27 = 29.6 percent), when young ferrets were released into the same colonies that were then vacant.

Discussion

Use of Habitats Other than Prairie Dog Colonies

The term “preference” suggests that use is compared to availability, but we made no explicit attempt to define or measure availability of habitat not occupied by prairie dogs. Noncolony areas, however, were much more available to ferrets (on a large scale at least) than were prairie dog colonies. Thus, the extremely high use of prairie dog colonies by black-footed ferrets does indeed suggest strong preference, and there was no need to delve into more rigorous analyses of preference at that large scale.

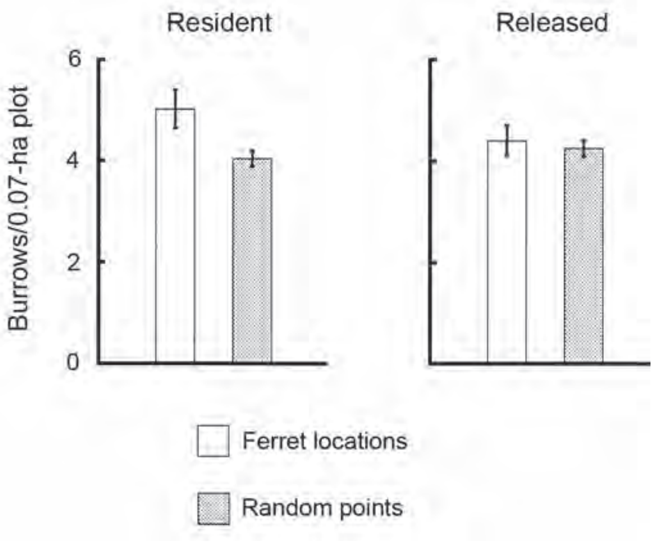

Figure 9. Densities of burrows (mean ± SE) in areas used by (and available to) black-footed ferret (*Mustela nigripes*) kits released into ferret-occupied habitat at Hawley Flats Mont., in 1997, and densities of burrows in habitat used by (and available to) the resident wild-born ferret kits at that site.

Figure 10. Densities of burrows (mean ± SE) in areas used by (and available to) the first black-footed ferret (*Mustela nigripes*) kits released at Locke Ranch and Hawley Flat, Mont., in 1994 and 1995, and densities of burrows in areas used by (and available to) ferret kits after subsequent releases during those years at those sites.

Most ferrets tracked during this study were young of the year, and many were captive-born ferrets released onto prairie dog colonies. To learn about their new surroundings, these naive animals must explore, and some may adopt home ranges that include multiple colonies. Thus, the small proportion of telemetric fixes away from prairie dog colonies is mostly explained by behaviors that should be expected even for a species fully dependent on prairie dogs. Also, a greater proportion of off-colony fixes occurred in the 1997 animals

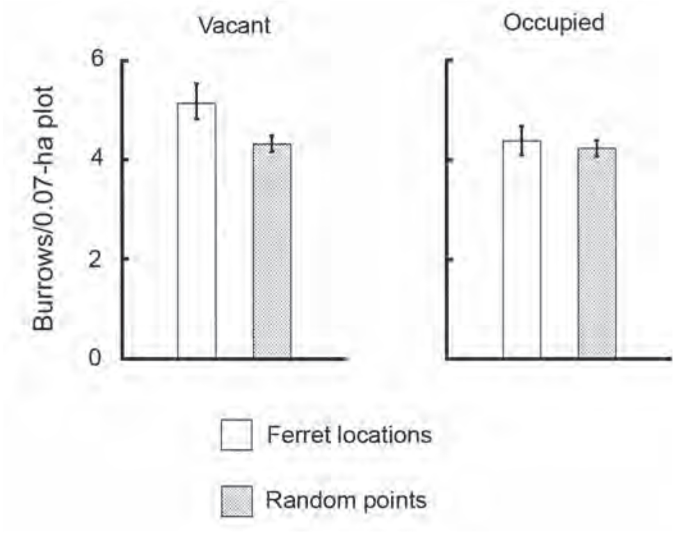

Figure 11. Densities of burrows (mean ± SE) in areas used by (and available to) black-footed ferret (*Mustela nigripes*) kits released into ferret-unoccupied habitat at Hawley Flat, Mont., in 1995, and densities of burrows in areas used by (and available to) ferret kits released to augment the extant population in 1997.

(16.7 percent), which were subjected to potentially more intense intraspecific competition than were the ferrets released into unoccupied habitat in 1994 and 1995. Considering that the remaining small proportion of "unexplained" off-colony moves also involved (1) ferrets that were killed by predators and carried away from colonies, (2) ferrets with whom telemetric contact was lost, rendering their future travels and fates unknown, (3) predominantly captive-reared ferrets that may behave erratically at times, and (4) dispersal that ultimately may lead ferrets to other prairie dog colonies, there was little indication that ferrets will attempt to live on habitat other than prairie dog colonies, let alone successfully colonize other habitats. We documented a high degree of preference for prairie dog colonies by ferrets, which weakens the contention that there should be a "broader range of possibilities for conservation of the black-footed ferret" (Owen and others, 2000, p. 422), an argument implying broader habitat tolerances based on similarities between black-footed ferrets and Siberian polecats (*Mustela eversmannii*) and the hypothetical niches of North American Pleistocene and Holocene ferrets (or polecats). Our data and those of others (e.g., Biggins, 2000) suggest that natural selection has resulted in considerable divergence of behaviors and nonskeletal features in these two extant species of *Mustela* and that they are "ecological equivalents" (Hoffman and Pattie, 1968, p. 57; Lincoln and others, 1998, p. 94) only in the broadest sense. Attempts to release each species on varying habitats further test this hypothesis. Reproductively sterile Siberian polecats persisted for only short periods when released on prairie dog colonies in Wyoming (16 percent survival for 15 days) and Colorado (16 percent survival for 1 day) (Biggins, 2000), and some of the polecats used habitats other than the prairie dog colonies. Release of Siberian polecats and black-footed ferrets into colonies of larger species of North American ground squirrels (*Spermophilus*) has not been attempted but could be informative.

Preferences Within Prairie Dog Colonies

For analyses of habitat preference within colonies, we defined as available to a ferret all of the prairie dog colony on which it resided. Definitions of availability are always somewhat arbitrary but are important because they affect the outcome of preference analyses (Johnson, 1980). Prior studies of ferret movements (Biggins and others, 1985, 1999; Biggins, 2000), coupled with the relatively small sizes of the colonies of the present study, helped justify our definition. We believe that the subjects of our study would not have been physically impeded from accessing any portion of the colonies on which they resided and were influenced primarily by the variables targeted for study (quality of habitat and competition for it). Even within the boundaries of prairie dog colonies, therefore, ferrets consistently preferred areas with relatively high densities of prairie dog burrows.

The preference of black-footed ferrets for areas on prairie dog colonies with high densities of prairie dog burrows was made possible by the clumped dispersion of burrows at our study sites. This nonrandom and nonuniform arrangement of burrow openings may be due to phenomena at several scales. Habitat quality for prairie dogs themselves may vary within the boundaries of their colonies, resulting from variation in soil type, soil depth, slope, and aspect. Vegetative mosaics are apparent on some colonies, resulting from these edaphic and physiographic attributes and other influences (e.g., plant competition) and from grazing by prairie dogs. Thus, the patchiness we observed at the scale of our plots (707 m^2) is likely a reflection of the patchiness at intermediate scales (measured in hectares) resulting from the factors mentioned above coupled with variation at finer scales caused (at least in part) by the social organization of black-tailed prairie dogs into coteries and by interconnected burrow openings within coteries (Hoogland, 1995). We believe that attention to these considerations of scale will be increasingly important in gaining a more complete understanding of ferret ecology. Former evaluations of habitat for black-footed ferrets (e.g., Hillman and others, 1979; Forrest and others, 1985; Houston and others, 1986; Miller and others, 1988; Biggins and others, 1993) heavily emphasized the larger scales of colonies and complexes and may have led us to overlook details important to ferrets. Ferret preferences for areas of relatively high densities of prairie dog burrows, and the apparent intraspecific competition for those areas, imply qualities that may be related to fitness. We hypothesize that the value of clusters of burrow openings lies not only in their correlation to clusters of prairie dogs as prey but also in the immediacy of protective cover from predators during aboveground movements by ferrets. Predation appears to be a substantial hazard for ferrets (Forrest and others, 1988; Biggins, 2000), causing by far the most losses during the repatriation program (Biggins, Godbey, Livieri, and others, this volume). Because of the positive association between safety and resources, ferrets are not forced into tradeoffs requiring choices between “a productive, but risky habitat and a less productive, safer habitat” (Grand and Dill, 1999, p. 389).

Intraspecific Competition for Habitat

Several lines of previous evidence suggest that territoriality is an important feature in the social lives of black-footed ferrets. Although direct agonistic encounters between free-ranging individual ferrets are rarely seen (Clark and others, 1986), two adult males were observed in what was described as “mortal combat” at the UL Bend in 1997 (Stoneberg, 1997, p. 13). Play behaviors in juveniles that may be precursors to such behaviors in adults (Poole, 1966, 1967, 1974) were commonly seen in free-ranging (Hillman, 1968; Clark and others, 1986) and captive (Miller, 1988; Vargas, 1994) litters. Agonistic behaviors between captive adult black-footed ferrets resembled agonistic interactions of domestic ferrets (Miller, 1988). General spacing patterns suggest that ferrets occupy somewhat distinct territories (Clark, 1989). Scent marking is a common behavior in ferrets and is particularly evident for males during the breeding season (Miller, 1988). Our understanding of competition among ferrets (especially females) for resources or space is nevertheless incomplete. Although free-ranging ferrets tend to occupy space that is not used by other ferrets of the same sex, occasional sharing of space by females during winter (Richardson and others, 1987) and even by females with litters (Paunovich and Forrest, 1987) raises doubts about exclusiveness of areas of activity. Captive Siberian polecats have been held in large cages for prolonged periods as same-sex and mixed-sex groups, but, on other occasions, aggression has been immediate and severe when multiple polecats were introduced into the same space (D. Biggins, unpub. data, 1995). Individual black-footed ferrets have severely injured their neighbors in conflicts through the wire mesh that separated their adjacent outdoor pens, and female ferrets have even killed their prospective mates (A. Vargas, oral commun., 1995). Simple rules seem inadequate for predicting outcomes of interactions. For females especially, activity area sizes and their exclusivity in time and space may be influenced by habitat quality and variation among individuals (Biggins, 2000), and perhaps nepotism at times masks the central tendency of ferrets to defend territories.

Nonetheless, the general theme of competition among black-footed ferrets for possession of space was supported by our study; the group that was predicted to be subordinate based on prior residency consistently occupied the habitat of lower quality. Large body size may be an advantage in contests, but we did not detect a significant effect of mass in the competition for high-quality habitat among sequentially released young ferrets. Ferrets seemed to follow the “bourgeois strategy” (Ramsay and Ratcliffe, 2003, p. 120) in which prior residency overwhelms effects of size and other factors. The duration of prior residency also may have an effect (Harwood and others, 2003). In an experiment involving releases of white-throated sparrows (*Zonotrichia albicollis*) into outdoor aviaries, Dearborn and Wiley (1993) noted a gradual increase in effect of prior residency from 2–45 days, but the increase was most dramatic during the first 14 days. Duration of prior residency for ferrets in our sequential release experiment was fairly brief, with 2–4 weeks between the first and subsequent releases, but duration of residency was >1 year for individuals in the extant population that was augmented in 1997.

As ferret populations are assembled through progressive releases and additions of wild-born animals, intraspecific competition appears to result in sequential occupation of habitat patches by descending order of burrow (and prey) density. As available habitat becomes filled, the additional occupancy of sites with lower densities of burrows and prairie dogs is expected to increase the variance in burrow density of occupied sites. At sites with low burrow densities, areas of activity of ferrets may be largest. These phenomena outwardly resemble the characteristics associated with an ideal free distribution or an ideal dominance (despotic) distribution (Fretwell and Lucas, 1970). Explorations by released ferrets may be sufficient to impart “ideal” knowledge regarding availability of habitat, but territoriality of resident ferrets may prevent “free” choice (sensu Fretwell and Lucas, 1970). Further assessment of processes involved in ferret habitat occupancy in relation to theoretical distributions (Fretwell and Lucas, 1970; Fretwell, 1972) must consider relative fitness (Messier and others, 1990; Beckman and Berger, 2003), a topic we will address separately with other data sets.

Commonly used habitat evaluation systems for black-footed ferrets (e.g., that of Biggins and others, 1993) likely overestimate ferret densities attainable on the best habitats. As acknowledged by Biggins and others (1993, p. 75) in the introduction to their suggested model, “Social behavior may dictate a maximum ferret density regardless of prey abundance.” Mounting evidence regarding territoriality in ferrets does indeed suggest that models used to predict carrying capacity of habitat for ferrets should include an increasing effect of social exclusion of ferrets at high densities of prairie dogs. Because the best quality habitats as rated by the model of Biggins and others (1993) are presently sustaining ferrets at densities almost double those of low-quality habitats, we suggest retention of the fundamental structure of the model, with modifications recently suggested (Biggins, Lockhart, and Godbey, this volume). Although our comparative data suggest that competitiveness varies among individuals and has an important influence on population assembly (groups varied in their ability to control space and resources), we are unable to estimate the strength of territoriality at varying prey densities.

Additional studies on territoriality in male and female ferrets could help refine predictions of the model at high prairie dog densities. The model also would benefit from an improved understanding of habitat limitations for reproductive female ferrets inhabiting colonies with low prairie dog densities, a subject beyond the scope of this study.

The prior residency advantage raises other issues of conservation concern. Quality of ferrets released may vary because of prerelease experience (Biggins and others, 1998, 1999) and age (Biggins, Godbey, Livieri, and others, this volume). Preliminary releases of lower quality animals may reduce the amount of good habitat available for higher quality animals subsequently released if the first animals become established. Even if those first residents succumb rather quickly to predation, their initial presence could elevate the risk to newcomers during the first critical days postrelease. Thus, we recommend careful consideration be given to choice of sites and sequence of release when habitat will receive groups of ferrets varying in prerelease experience, origin, and age.

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References Cited

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Beckman, J.P., and Berger, J., 2003, Using black bears to test ideal-free distribution models experimentally: Journal of Mammalogy, v. 84, p. 594–606.

Berry, K.J., and Mielke, P.W., Jr., 1985, Subroutines for computing exact Chi-square and Fisher's exact probability tests: Education and Psychological Measurement, v. 45, p. 153–159.

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Biggins, D.E., Schroeder, M., Forrest, S., and Richardson, L., 1985, Movements and habitat relationships of radio-tagged black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 11.1–11.17.

Biggins, D.E., Schroeder, M.H., Forrest, S.C., and Richardson, L., 1986, Activity of radio-tagged black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 135–140.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Campbell, T.M., III, Clark, T.W., Richardson, L., Forrest, S.C., and Houston, B.R., 1987, Food habits of Wyoming black-footed ferrets: American Midland Naturalist, v. 117, p. 208–210.

Clark, T.W., 1989, Conservation biology of the black-footed ferret *Mustela nigripes*: Philadelphia, Pa., Wildlife Preservation Trust International, Wildlife Preservation Trust Special Scientific Report No. 3, 175 p.

Clark, T.W., Richardson, L., Forrest, S.C., Casey, D.E., and Campbell, T.M., III, 1986, Descriptive ethology and activity patterns of black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 115–134.

Davies, N.B., 1978, Territorial defence in the speckled wood butterfly (*Pararge aegeria*)—the resident always wins: Animal Behaviour, v. 26, p. 138–147.

Dearborn, D.C., and Wiley, R.H., 1993, Prior residence has a gradual influence on dominance in captive white-throated sparrows: Animal Behaviour, v. 46, p. 39–46.

Ewer, R.F., 1973, The carnivores: Ithaca, N.Y., Cornell University Press, 494 p.

Flath, D.L., and Clark, T.W., 1986, Historic status of black-footed ferret habitat in Montana: Great Basin Naturalist Memoirs No. 8, p. 63–71.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Forrest, S.C., Clark, T.W., Richardson, L., and Campbell, T.M., III, 1985, Black-footed ferret habitat—some management and reintroduction considerations: Cheyenne, Wyoming BLM Wildlife Technical Bulletin No. 2, 49 p.

Fretwell, S.D., 1972, Populations in a seasonal environment: Princeton, N.J., Princeton University Press, Monographs in Population Biology 5, 217 p.

Fretwell, S.D., and Lucas, H.L., 1970, On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development: Acta Biotheoretica, v. 19, p. 16–36.

Grand, T.C., and Dill, L.M., 1999, Predation risk, unequal competitors and the ideal free distribution: Evolutionary Ecology Research, v. 1, p. 389–409.

Harwood, A.J., Griffiths, S.W., Metcalfe, N.B., and Armstrong, J.D., 2003, The relative influence of prior residency and dominance on the early feeding behaviour of juvenile Atlantic salmon: Animal Behaviour, v. 65, p. 1141–1149.

Hillman, C.N., 1968, Field observations of black-footed ferrets in South Dakota: Transactions of the North American Wildlife and Natural Resources Conference, v. 33, p. 433–443.

Hillman, C.N., Linder, R.L., and Dahlgren, R.B., 1979, Prairie dog distributions in areas inhabited by black-footed ferrets: American Midland Naturalist, v. 102, p. 185–187.

Hoffman, R.S., and Pattie, D.L., 1968, A guide to Montana mammals: Missoula, University of Montana, 133 p.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing mammal: Chicago, University of Chicago Press, 557 p.

Houston, B.R., Clark, T.W., and Minta, S., 1986, Habitat suitability index model for the black-footed ferret—a method to locate transplant sites: Great Basin Naturalist Memoirs No. 8, p. 99–114.

Howe, R.W., Davis, G.J., and Mosca, V., 1991, The demographic significance of ‘sink’ populations: Biological Conservation, v. 57, p. 239–255.

Jennions, M.D., and Backwell, P.R.Y., 1996, Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*: Biological Journal of the Linnean Society, v. 57, p. 293–306.

Johnson, D.H., 1980, The comparison of usage and availability measurements for evaluations of resource preference: Ecology, v. 61, p. 65–71.

Krohn, W.B., 1992, Sequence of habitat occupancy and abandonment—potential standards for testing habitat models: Wildlife Society Bulletin, v. 20, p. 441–444.

Lincoln, R., Boxshall, G., and Clark, P., 1998, A dictionary of ecology, evolution, and systematics: United Kingdom, Cambridge University Press, 361 p.

Linder, R.L., Dahlgren, R.B., and Hillman, C.N., 1972, Black-footed ferret–prairie dog interrelationships, *in* Symposium on rare and endangered wildlife of the Southwestern United States: Santa Fe, New Mexico Department of Game and Fish, p. 22–37.

Mathis, A., Schmidt, D.W., and Medley, K.A., 2000, The influence of residency status on agonistic behavior of male and female Ozark zigzag salamanders *Plethodon angusticlavius*: American Midland Naturalist, v. 143, p. 245–249.

Messier, F.J., Virgl, A., and Marinelli, L., 1990, Density-dependent habitat selection in muskrats—a test of the ideal free distribution model: Oecologia, v. 84, p. 380–385.

Miller, B., Reading, R.P., and Forrest, S., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Miller, B.J., 1988, Conservation and behavior of the endangered black-footed ferret (*Mustela nigripes*) with a comparative analysis of reproductive behavior between the black-footed ferret and the congeneric domestic ferret (*Mustela putorius furo*): Laramie, University of Wyoming, Ph.D. dissertation, 195 p.

Miller, B.J., Menkens, G.E., and Anderson, S.H., 1988, A field habitat model for black-footed ferrets, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: USDA Forest Service, General Technical Report RM-154, p. 98–102.

Neumann, D.R., 1999, Agonistic behavior in harbor seals (*Phoca vitulina*) in relation to the availability of haul-out space: Marine Mammal Science, v. 15, p. 505–525.

Owen, P.R., Bell, C.J., and Mead, E.M., 2000, Fossils, diet, and conservation of black-footed ferrets (*Mustela nigripes*): Journal of Mammalogy, v. 81, p. 422–433.

Paunovich, R., and Forrest, S.C., 1987, Activity of a wild black-footed ferret litter: Prairie Naturalist, v. 19, p. 159–162.

Poole, T., 1966, Aggressive play in polecats: Symposia of the Zoological Society of London, v. 18, p. 23–44.

Poole, T., 1967, Aspects of aggressive behavior in polecats: Zeitschrift für Tierpsychology, v. 24, p. 351–369.

Poole, T., 1974, Detailed analysis of fighting in polecats, Mustelidae, using cine film: Journal of the Zoological Society of London, v. 173, p. 369–393.

Powell, R.A., 1979, Mustelid spacing patterns—variations on a theme by *Mustela*: Zeitschrift für Tierpsychology, v. 50, p. 153–165.

Pulliam, H.R., and Danielson, B.J., 1991, Sources, sinks, and habitat selection—a landscape perspective on population dynamics: The American Naturalist, v. 137, p. S50–S66.

Ramsay, S.M., and Ratcliffe, L.M., 2003, Determinants of social rank in female black-capped chickadees (*Poecile atricapilla*): Canadian Journal of Zoology, v. 81, p. 117–121.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming (USA): American Midland Naturalist, v. 117, p. 225–239.

Ricklefs, R.E., 1990, Ecology (3d ed.): New York, W.H. Freeman and Company, 896 p.

Riechert, S.E., 1978, Games spiders play—behavioural variability in territorial disputes: Behavioural Ecology and Sociobiology, v. 3, p. 135–162.

Sheets, R.G., Linder, R.L., and Dahlgren, R.B., 1972, Food habits of two litters of black-footed ferrets in South Dakota: American Midland Naturalist, v. 87, p. 249–251.

Stoneberg, R., 1997, Montana black-footed ferret reintroduction program: 1996–1997 progress report: Helena, Montana Department of Fish, Wildlife and Parks, 21 p.

Vargas, A., 1994, Ontogeny of the endangered black-footed ferret (*Mustela nigripes*) and effects of captive upbringing on predatory behavior and post-release survival: Laramie, University of Wyoming, Ph.D. dissertation, 272 p.

Wiens, J.A., 1976, Population responses to patchy environments: Annual Review of Ecology and Systematics, v. 7, p. 81–120.

25.09.2005

Evaluating Habitat for Black-footed Ferrets: Revision of an Existing Model

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Abstract

Black-footed ferrets (*Mustela nigripes*) are highly dependent on prairie dogs (*Cynomys* spp.) as prey, and prairie dog colonies are the only known habitats that sustain black-footed ferret populations. An existing model used extensively for evaluating black-footed ferret reintroduction habitat defined complexes by interconnecting colonies with 7-km line segments. Although the 7-km complex remains a useful construct, we propose additional, smaller-scale evaluations that consider 1.5-km subcomplexes. The original model estimated the carrying capacity of complexes based on energy requirements of ferrets and density estimates of their prairie dog prey. Recent data have supported earlier contentions of intraspecific competition and intrasexual territorial behavior in ferrets. We suggest a revised model that retains the fixed linear relationship of the existing model when prairie dog densities are <18/ha and uses a curvilinear relationship that reflects increasing effects of ferret territoriality when there are 18–42 prairie dogs per hectare. We discuss possible effects of colony size and shape, interacting with territoriality, as justification for the exclusion of territorial influences if a prairie dog colony supports only a single female ferret. We also present data to support continued use of active prairie dog burrow densities as indices suitable for broad-scale estimates of prairie dog density. Calculation of percent of complexes that are occupied by prairie dog colonies was recommended as part of the original habitat evaluation process. That attribute has been largely ignored, resulting in rating anomalies.

Keywords: black-footed ferret, burrows, carrying capacity, competition, *Cynomys*, energy, habitat, *Mustela nigripes*, prairie dog, territory

Introduction

By 1988, captive breeding of black-footed ferrets (*Mustela nigripes*) rescued from a failing population in Wyoming was becoming successful (Biggins and others, 1997), and a subcommittee of the Black-footed Ferret Interstate Coordinating Committee (ICC) addressed the challenge of locating, evaluating, and comparing sites for black-footed ferret reintroduction. Habitat for terrestrial species, including prairie dogs (*Cynomys* spp.), is commonly evaluated with respect to vegetative and physiographic features. Although we recognize the crucial link between prairie dogs and their environments, the extreme specialization of the black-footed ferret allows us to equate black-footed ferret habitat with prairie dog colonies. A habitat model now in common use was developed by the ICC to assess the ability of prairie dog colonies and complexes to support populations of black-footed ferrets (Biggins and others, 1993). The model arose from earlier descriptions and models of ferret habitat (Linder and others, 1972; Hillman and others, 1979; Forrest and others, 1985; Houston and others, 1986; Miller and others, 1988), models of ferret energetics (Stromberg and others, 1983; Powell and others, 1985), data on ferret nutrition and food habits (Sheets and others, 1972; Campbell and others, 1987; Joyce, 1988), and information on behaviors of free-ranging ferrets (Hillman, 1968; Biggins and others, 1985; Paunovich and Forrest, 1987; Richardson and others, 1987). Biggins and others (1993) also provided a method for estimating approximate densities of prairie dogs from strip transect samples of active burrows and offered a technique for grouping colonies into complexes. Complexes were defined as clusters of colonies that could be circumscribed with 7-km line segments; colonies are sequentially added to a complex if they are separated by ≤7 km. Spaces within a complex that are devoid of prairie dogs are defined similarly.

We herein suggest changes to procedures described by Biggins and others (1993), based in part on information collected during 1991–2003 from reintroduced populations of black-footed ferrets, and we discuss aspects of the existing system needing renewed emphasis. Changes include assessing portions of complexes at a smaller scale (called subcomplexes), incorporating the effects of ferret territoriality

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in assessments of habitat carrying capacity, and limiting the effect of ferret territoriality on small habitat patches where social strife is unlikely to influence ferret use.

Subcomplexes

The initial impetus for considering smaller, more compact clusters of prairie dog colonies as subcomplexes stemmed from de facto procedures used to select and prioritize ferret release sites. Sites were intuitively regarded as high quality if colonies were closely spaced or large and if prairie dog densities were high. Release of ferrets took place on such "core" sites, with much less attention given to the remainder of the complex as defined by the 7-km procedure (Biggins and others, 1993). We describe a process, involving subcomplexes, that has been in practical use since 1999 by the U.S. Fish and Wildlife Service and partners to allocate ferrets.

On occasion, more than one cluster of colonies has been used as a release site, but ferret releases in each year have been conducted on relatively small portions of complexes. Following initial release(s), ferrets rather quickly populated some of these core release areas through natural reproduction; other clusters in a complex defined with the 7-km criterion were mostly populated with additional releases (e.g., Conata Basin, S. Dak.) or natural dispersal over longer time periods (Shirley Basin, Wyo.). Although lines of delineation are arbitrary, ferret movement within clusters where colonies were separated by ≤1.5 km was common. At UL Bend National Wildlife Refuge, Mont., for example, there were 88 intercolony moves by radio-tagged ferrets during 1994, 1995, and 1997 (Biggins, Godbey, Matchett, and Livieri, this volume); 77 (85.5 percent) of these moves were between colonies separated by <1.5 km, but all moves were between colonies separated by <2.1 km. In the Meeteetse, Wyo., complex of white-tailed prairie dogs (*Cynomys leucurus*) that supported the remnant ancestral population of ferrets, most colonies were interconnected with a 1.5-km maximum distance between them. Based on these experiences and data, we propose defining a subcomplex as a group of colonies that can be linked to one another with a series of line segments ≤1.5 km in length. The procedure for outlining a subcomplex will be further standardized by following the method used to circumscribe a complex (Biggins and others, 1993), but substituting a 1.5-km line segment for the 7-km line segment (fig. 1).

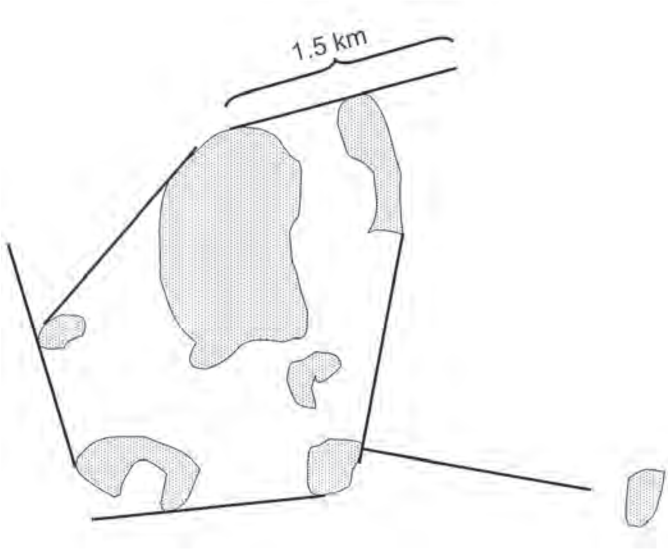

Figure 1. Procedure for circumscribing a subcomplex of prairie dog (*Cynomys* spp.) colonies by using a minimum intercolony distance of 1.5 km. See Biggins and others (1993) for additional details on the methodology.

Territoriality and Carrying Capacity

Carrying capacity has been traditionally discussed in terms of populations of an organism and their food supply, with implications of sustainability of resources (Leopold, 1933). In that sense, the habitat model of Biggins and others (1993) attempts to estimate carrying capacity of prairie dog colonies for black-footed ferrets. Many organisms, however, seem to space themselves within habitat. Carnivores are often intrasexually territorial, but King's (1990) chapter on "adjustable living spaces" provides evidence that there is an interaction between habitat quality (mainly abundance of prey) and territoriality for other *Mustela* species. The utility of estimating the upper limits of habitat to sustain organisms, whether such limits are imposed by food or other mechanisms, was evident in early attempts to model regulated growth with the logistic equation (Pearl and Reed, 1920) and in Leopold's (1933) discussions of managing game for sustained yields. More recent efforts at modeling ferret population fluctuations require similar input (Bevers and others, 1997).

Although somewhat conflicting evidence precluded considering ferret territoriality in their earlier model, Biggins and others (1993, p. 75) suggested that "social behavior may dictate a maximum ferret density regardless of prey abundance." There is increasing evidence that black-footed ferret territoriality does indeed constrain predictions of the energetics model when prey may not be limiting. First, reintroduced ferret populations in South Dakota habitats seldom had average densities exceeding about 1 female per 30 ha, even though the energetics-based model often predicted 1 female per 20 ha or less. Additional evidence from ferrets released in Montana and South Dakota suggests that there is competition for good quality habitat (Biggins, Godbey, Matchett, and Livieri, this volume). These recent results are consistent with observations that female ferrets generally do not use overlapping areas (Richardson and others, 1987) and evidence of spacing in other *Mustela* species (Powell, 1979; King, 1990). The mounting evidence is sufficiently compelling that we here suggest adding a function to the simple linear relationship between densities of black-footed ferrets and prairie dogs that will have increasing impact as ferret density rises. A guiding principle is parsimony; we do not suggest adding complexity that is unsupported empirically.

We revised the energetics-based model (Biggins and others, 1993) to allow an effect of territoriality that is initiated at densities of 18 prairie dogs per hectare, gradually increases in intensity, and reaches an asymptote of 0.04 ferret families per hectare at a prairie dog density of 42/ha (fig. 2). Because a black-footed ferret family includes one female, we are discussing female ferret density. A quadratic equation ($Y = a + bX + cX^2$) adequately approximates the proposed curvilinear relationship within the range 18–42 prairie dogs per hectare, where: Y = predicted density of female ferrets, X = density of prairie dogs, a = -0.00456329, b = 0.00193283, and c = -0.00002083. If there are <18 prairie dogs per hectare, the equation for the straight line segment of the graph remains $Y = 0.00131062X$, a slope determined by the existing energetically based estimates and a linear relationship between ferret density and prairie dog density. Although white-tailed prairie dogs occasionally have been found at densities >20/ha, the graph suggests (correctly, we believe) that density of female ferrets seldom will be limited by territoriality on white-tailed prairie dog habitat. In contrast, we believe that territorial behavior of female ferrets will commonly influence their spacing on most black-tailed prairie dog (*Cynomys ludovicianus*) habitat. Under our proposed relationship, that influence will increase until female ferrets reach densities of about 1 ferret per 25 ha of habitat (the maximum density of 0.04 ferrets per hectare). We predict that prairie dog densities above 42/ha will not result in increased densities of territorial female ferrets, but these higher densities of prairie dogs may affect other population attributes such as ferret survival and productivity.

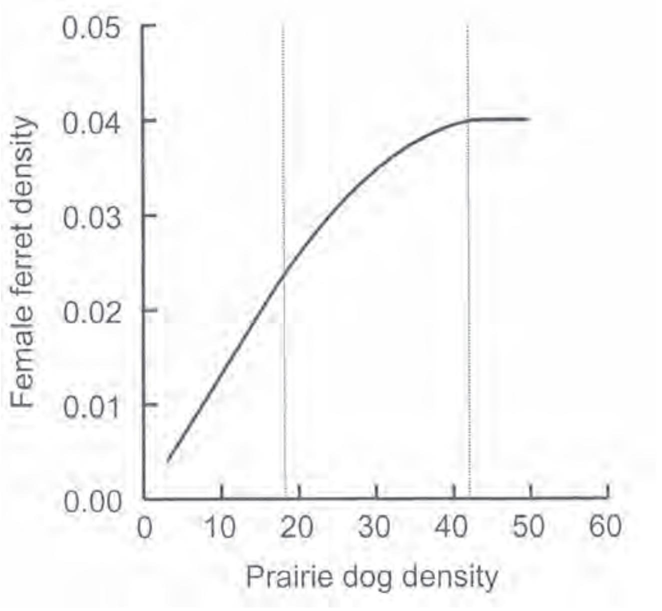

Figure 2. Hypothetical relationship between densities of prairie dogs (*Cynomys* spp.) and densities of female black-footed ferrets (*Mustela nigripes*) (individuals/ha), allowing territoriality to modify the linear relationship predicted by the energetics-based equation ($Y = X/763$) of Biggins and others (1993) at prairie dog densities >18/ha but defining an upper limit of 0.04 ferrets/ha. At intermediate prairie dog densities (18–42/ha), the increasing influence of territoriality is approximated by the quadratic equation $Y = a + bX + cX^2$, where Y = density of ferrets, X = density of prairie dogs, a = -0.00456329, b = 0.00193283, and c = -0.00002083.

Habitat-induced Isolation

"Islands" or "peninsulas" of habitat with high densities of prairie dogs may support more ferret families than would large blocks of uniform habitat because some configurations of habitat can reduce among-female interaction. An "island" arrangement with a colony small enough to support just one female and her litter (figs. 3 and 4) seems likely to eliminate any potential for limiting effects of territoriality. A "peninsula" configuration removes that effect on two sides, but territorial spacing comes into play for end-to-end territories along linear habitat. The example of 20 ha of prairie dog colony needed to support a female and her litter (fig. 3) is somewhat conservative. Five of the nine ferret litters reported by Hillman and others (1979) in Mellette County, S. Dak., were raised on colonies <16 ha in area (one was 10 ha). A female ferret raised two kits on a 5-ha colony in Montana (fig. 4); however, it seems doubtful that the Montana female could have accomplished that feat without seriously depleting the prairie dog population, and her small litter suggests that conditions may have been suboptimal. At Meeteetse, Wyo., the smallest colonies that supported females with litters were about 50 ha, but white-tailed prairie dogs at Meeteetse occurred at much lower densities (about 7.7/ha, calculated from the visual count density of Clark and others (1985) divided by the sightability adjustment of 0.495 of Biggins and others (1993)) than did the black-tailed prairie dogs discussed above (Hillman and Linder, 1973). We accommodate the most extreme of these influences of colony sizes and shapes into the evaluation procedure with a provision that removes the effect of territoriality if a colony is sufficiently small and isolated to support just a single female. To facilitate evaluation of prairie dog complexes as habitat for black-footed ferrets, a spreadsheet with appropriate formulae is available from the authors.

Colonies as small as the minimum mapping unit (5 ha) suggested by Biggins and others (1993) may support a female and her litter. Usually, however, colonies <10 ha will not have sufficient numbers of prairie dogs to sustain both themselves and a ferret family. Depletion of prairie dogs can be expected on colonies <10 ha if they are occupied by a ferret family, and it seems unlikely that such small colonies will support ferret reproduction in consecutive years. Nevertheless, we propose allowing colonies as small as 5 ha to contribute to the family rating of a complex by using the direct linear equation (Biggins and others, 1993), without the influence of

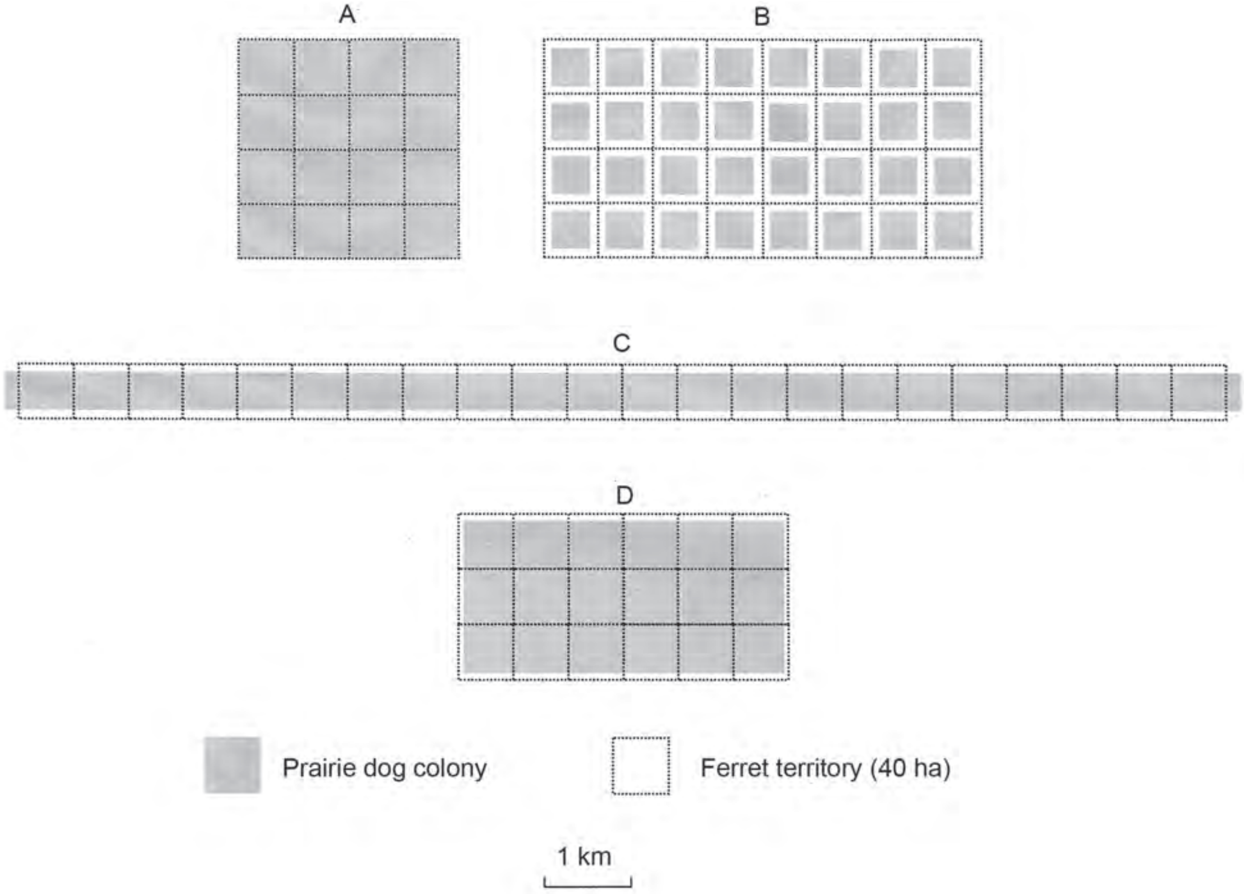

Figure 3. Comparison of female black-footed ferret (*Mustela nigripes*) numbers supported by hypothetical prairie dog (*Cynomys* spp.) complexes occupying 640 ha: (A) a complex with a single square colony (*n* = 16 ferrets); (B) a complex with 20-ha colonies at sufficient spacing to allow separate ferret territories (*n* = 32 ferrets); (C) a complex with a single linear colony (22 ferrets); and (D) a complex with a single rectangular colony (18 ferrets). These predictions are based on the following assumptions: (1) ferret territories are 40-ha squares, (2) a patch of prairie dog habitat occupying at least 20 ha is centered in the territory, and (3) a habitat patch of 20 ha has sufficient prairie dogs to sustain a ferret family while maintaining its prairie dog population.

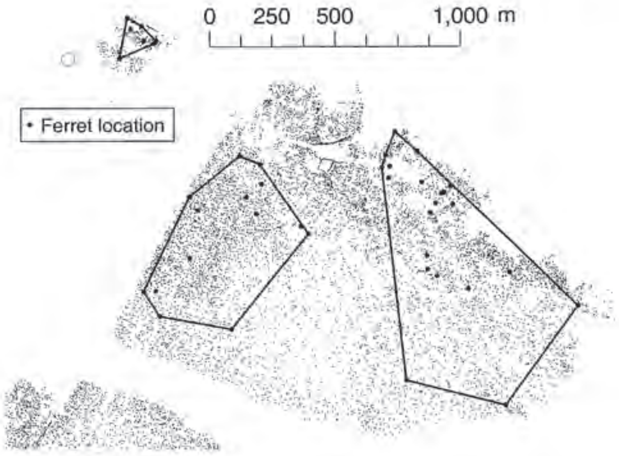

Figure 4. Activity areas (circumscribed by minimum convex polygons) for three female black-footed ferrets (*Mustela nigripes*) with litters. These females and their litters were repeatedly relocated during summer 1998 at UL Bend National Wildlife Refuge, Mont. Heterogeneity in dispersion of black-tailed prairie dog (*Cynomys ludovicianus*) burrows (small dots) is evident. The female ferret on the small colony is relatively insulated from repeated contact with other females. In this example, areas of dense prairie dog burrows do not form true "islands" of good habitat, but low densities of prairie dog burrows in the central portion of the larger colony may have influenced separation of ferret activity areas.

territoriality. If the rating using the linear equation is less than two female ferrets, then a single colony, regardless of size or prairie dog density, may be evaluated with the linear relationship (even if the result is a rating <1.0).

The concept of islands and peninsulas discussed above creates an image of prairie dog colonies within landscapes that have areas devoid of prairie dogs. Islands with high densities of prairie dogs, however, may also be situated within intervening habitat of low prairie dog density. Thus, the island effect may be operative within colonies that have heterogeneous densities of prairie dogs. The mosaic of prairie dog densities is reflected by nonuniform densities of prairie dog burrows. Heterogeneity in distribution of burrows may influence separation of activity areas of at least some female ferrets (fig. 4).

Another Look at Burrow Densities as Indicators of Prairie Dog Density

Biggins and others (1993) suggested that densities of active burrows were significantly correlated with densities of prairie dogs determined from visual counts. Severson and Plumb (1998, p. 864), however, failed to detect a relationship between densities of prairie dogs and their burrows, concluding that “burrow counts . . . should not be used to estimate or index prairie dog numbers.” This theme has a rather long history of debate extending to species other than prairie dogs, and a full discussion is outside the intended scope of this paper. Nevertheless, an overview of the topic and brief discussion of the specific criticism noted above are appropriate because working groups responsible for monitoring ferret reintroduction sites have made wide use of burrow sampling to calculate indices of habitat quality for ferrets. The need remains for a practical technique to monitor prairie dog status and trends over large scales of space (thousands of hectares) and time (decades). Decisions to use some form of capture-recapture method, visual counts, or burrow indices to estimate prairie dog abundance and density depend in part on objectives and available resources (Biggins and others, 2006). In addition, choice of method will be affected by precision and accuracy required.

Biggins and others (1993) provided only correlation coefficients for regression relationships between data from burrow transects and visual counts. To enhance comparisons with other data sets, more information is needed. Their data sets were generated from counts and transects on 30 white-tailed prairie dog plots and 39 black-tailed prairie dog plots. Using regression models with constants (Biggins and others [1993] reported regression through the origin), the relationships between densities of active burrows and density of prairie dogs as determined by visual counts were highly significant for both species (white-tailed prairie dogs, $F_{1,28} = 86.282$, $P < 0.001$, $R^2 = 0.755$; black-tailed prairie dogs, $F_{1,37} = 29.390$, $P < 0.001$, $R^2 = 0.443$). A comparison of the studies done by Severson and Plumb (1998) and Biggins and others (1993) reveals differences in several key features that collectively may affect the power to detect correlations (table 1). Collectively, the relative ranges of values and various levels of sampling intensity (e.g., plot size, number of plots, geographic coverage) should have given an advantage to the data sets of Biggins and others (1993). Intensity of transect sampling to estimate burrow density is as important as other features but was not reported by Severson and Plumb (1998).

Evidence of the utility of the burrow transect technique is also provided by data generated from its use. The overall collapse of the Meeteetse complex of white-tailed prairie dogs was documented by using densities of active burrows derived from strip transect sampling (fig. 5). It would be difficult to imagine that the downward trend during the 10-year study was an artifact of the sampling procedure, even without the corroborative evidence that exists from visual counts (D.

Table 1. Attributes of two studies on the relationship between densities of black-tailed prairie dogs (*Cynomys ludovicianus*) and densities of their active burrows.

	Severson and Plumb (1989)	**Biggins and others (1993)**
Number of States	1	3
Number of plots	24	39
Plot size (ha)	4	9
Area sampled (ha)	96	351
Burrow transects (km)	?	248
Lowest prairie dog density (no./ha)	8	0.8
Highest prairie dog density (no./ha)	46	54.2

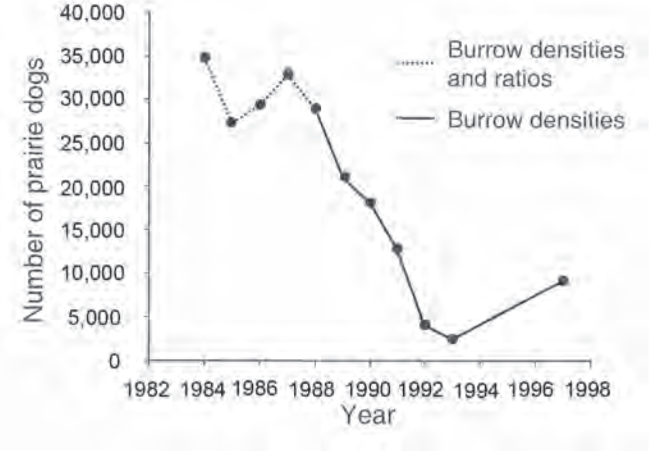

Figure 5. Estimates of white-tailed prairie dogs (*Cynomys leucurus*) on the Meeteetse, Wyo., complex, derived from estimates of active burrow density (Biggins and others, 1993). (Adapted from Biggins and Kosoy, 2001. Reprinted with permission of the *Journal of the Idaho Academy of Science*, Pocatello, Idaho.)

Biggins, unpub. data, 1988–93) that were repeated annually over most of that time period.

The purpose of the foregoing discussion is simply to provide evidence that burrow indices are a useful tool for indexing prairie dog abundance. This does not imply superiority of the technique compared to other tools; methods must be matched to objectives, size of area to be sampled, local conditions, and available funding.

Reemphasizing Percent of a Complex Occupied by Prairie Dog Colonies

Spatial relationships and shapes of prairie dog colonies were discussed above in the context of small islands and peninsulas of habitat with high prairie dog densities. Others (Forrest and others, 1985; Houston and others, 1986; Miller and others, 1988; Biggins and others, 1993) have discussed spatial arrangements of prairie dog colonies at larger scales, implying that some measure of colony arrangement or density within a complex is necessary to adequately evaluate habitat quality for black-footed ferrets. The 7-km limitation to intercolony spacing (Biggins and others, 1993) was a partial solution, but, without additional criteria, vast complexes that are thinly populated with prairie dog colonies may provide the same rating as complexes with more compact arrangements of colonies (fig. 6). There have been theoretical problems with measures of colony dispersion such as intercolony distances (Biggins and others, 1993), ultimately leading the ICC to adopt the conceptually simple tactic of using percent occupied (100 × sum of colony area/total area of complex) proposed by Miller and others (1988). During the first decade of ferret reintroductions, however, the spatial arrangement of prairie dog colonies within complexes largely has been ignored. Few participants have bothered to calculate the percent occupied attribute suggested as an overview of dispersion of colonies. By invoking the new procedure for defining subcomplexes of colonies spaced at 1.5 km or less, the consequences of this oversight are diminished (but not eliminated). It will be possible to examine how much of a complex consists of high-quality "core" subcomplexes. Subcomplexes should be rated separately from 7-km complexes; they should no longer be considered as having equal quality to complexes with the same cumulative area occupied by prairie dog colonies (fig. 6C versus 6A and 6B). Nevertheless, calculation of the proportion of complexes and subcomplexes occupied by prairie dog colonies will provide useful additional information (e.g., to distinguish between complexes such as A and B of fig. 6), and we continue to recommend that management teams at all reintroduction sites make these simple measurements. The technique will allow improved comparisons of complexes and subcomplexes among and within ferret reintroduction sites and may help characterize the potential for colony expansion.

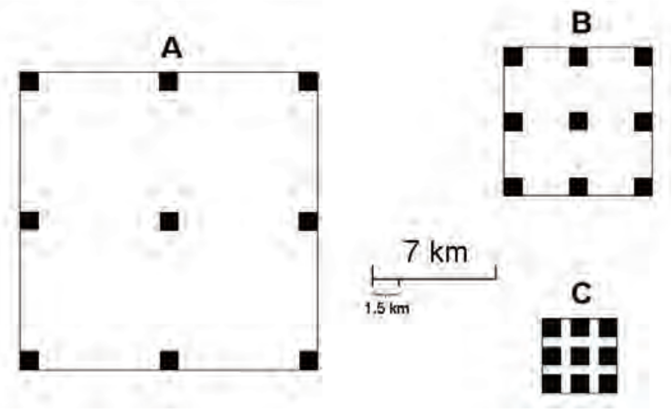

Figure 6. In these three hypothetical complexes, total area occupied by prairie dog (*Cynomys* spp.) colonies (shaded squares) is the same (1,000 ha), but the percentages of each complex occupied by colonies are 4%, 14%, and 57% for A, B, and C, respectively. Are the complexes of equal quality as habitat for black-footed ferrets (*Mustela nigripes*)? Arrangement C qualifies as a subcomplex because of intercolony spacing of <1.5 km.

Summary of the Procedure for Evaluating Ferret Habitat

The following steps for evaluating habitat for black-footed ferrets summarize the approach suggested by Biggins and others (1993) and the modifications presented herein.

1. Map the complex of prairie dog colonies.
2. Circumscribe the complex by using the 7-km criterion.
3. Circumscribe high-quality subcomplexes by using the 1.5-km criterion.
4. Estimate areas of complex, subcomplexes, and colonies with geographic information system (GIS) software if maps are digital. Use polar planimeter or other methods (e.g., dot grid) to estimate areas if only hard copies of maps are available.
5. Calculate percent of complex and subcomplexes occupied by prairie dog colonies.
6. Estimate prairie dog densities on colonies by using burrow density transects or visual counts.
7. Enter density and area estimates for each colony into separate spreadsheets for the overall complex and all subcomplexes.
8. Calculate ferret family ratings by using modified formulae (example spreadsheets with formulae are available from the authors).

Assumptions and Unresolved Questions

We believe that the suggested modifications discussed above will improve the existing model but reiterate that any model is only an approximation of reality (Biggins and others, 1993). Reflection on the basic assumptions involved in this exercise serves as a reminder of its inexact nature. Assumptions include (1) the average prairie dog weighs 760 g, (2) a ferret wastes 20 percent of each prairie dog it kills, (3) the several steps involved in estimating caloric demands of ferrets are correct, (4) losses of prairie dogs to other causes are 250 percent of losses caused by ferret predation, (5) the intrinsic rate of growth for prairie dog populations (λ) is 1.0, and (6) prairie dog populations remain stable. A sobering fact is that some of these attributes vary widely (e.g., numbers 4 and 5) and are in need of further study. The earlier model implicitly assumes that all prairie dogs, regardless of sex or age, are equally available as prey. If female ferrets selectively prey upon juvenile prairie dogs, their own productivity may be more closely correlated with prairie dog productivity than with prairie dog density. This possibility leads to questions about links between forage production, prairie dog production, and ferret production and highlights the potential importance of local and annual variation in precipitation.

A better understanding of prairie dog torpor (Lehmer and Biggins, 2005), burrow-plugging behavior, and energetics of ferret digging behavior could also improve the quality of these models. Is the digging involved in excavating hibernating prey more energetically costly than hunting of nonhibernating prey (Harrington and others, 2003)? What is the balance in tradeoffs between energetic costs of accessing prey and risk of injury in killing prey when comparing hibernating and nonhibernating prairie dogs? Does the presumably lower risk involved in killing hibernating prey allow use of larger prairie dogs that might not otherwise be available?

Territoriality in ferrets also remains poorly understood. Key questions include the following: (1) At what densities of prey does control of minimum space take precedence over control of prey resources? Can our proposed curve be further refined? (2) Does nepotism affect territory size and overlap (i.e., are females more tolerant of their female offspring than of less closely related females)? (3) How do shapes and arrangements of high-quality patches within and among colonies affect territorial behavior?

Some related topics would be appropriate for additional investigation. The earlier attempt to define minimum habitat attributes necessary to sustain female ferret reproduction (Biggins and others, 1993) may be questioned. Further study of female ferret behavior on white-tailed prairie dog or Gunnison's prairie dog (*Cynomys gunnisoni*) colonies, where prey densities are low, would help establish the lower limits. Preliminary data suggest a positive correlation between productivity of female ferrets and density of burrows in the habitat they occupy (D. Biggins, M. Matchett, and T. Livieri, unpub. data, 1997–2000), a relationship that also suggests further research on habitats with low prey densities. Territorial behavior of male ferrets has been ignored but may be an important factor in extinction risk for small populations (Conservation Breeding Specialist Group, 2004). Increasing numbers of black-footed ferrets in reintroduced populations are providing more opportunity to investigate these and other important aspects of ferret ecology.

References Cited

Bevers, M., Hof, J., Uresk, D.W., and Schenbeck, G.L., 1997, Spatial optimization of prairie dog colonies for black-footed ferret recovery: Operations Research, v. 45, p. 495–507.

Biggins, D.E., and Kosoy, M.Y., 2001, Disruptions of ecosystems in western North America due to invasion by plague: Journal of the Idaho Academy of Science, v. 37, p. 62–65.

Biggins, D.E., Miller, B.J., Clark, T.W., and Reading, R.P., 1997, Management of an endangered species—the black-footed ferret, *in* Meffe, G., and Carroll, R., eds., An introduction to conservation biology (2d ed.): Sunderland, Mass., Sinauer Associates, Inc., p. 420–426.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Biggins, D.E., Schroeder, M., Forrest, S., and Richardson, L., 1985, Movements and habitat relationships of radio-tagged black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 11.1–11.17.

Biggins, D.E., Sidle, J.G., Seery, D.B., and Ernst, A.E., 2006, Estimating the abundance of prairie dogs, *in* Hoogland, J.L., ed., Conservation of the black-tailed prairie dog: Washington, D.C., Island Press, p. 94–107.

Campbell, T.M., III, Clark, T.W., Richardson, L., Forrest, S.C., and Houston, B.R., 1987, Food habits of Wyoming black-footed ferrets: American Midland Naturalist, v. 117, p. 208–210.

Clark, T.W., Richardson, L., Forrest, S.C., Campbell, T.M., III, Casey, D., and Fagerstone, K.A., 1985, Black-footed ferret prey base, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 7.1–7.7.

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management planning workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

Forrest, S.C., Clark, T.W., Richardson, L., and Campbell, T.M., III, 1985, Black-footed ferret habitat—some management and reintroduction considerations: Cheyenne, Wyoming BLM Wildlife Technical Bulletin No. 2, 49 p.

Harrington, L.A., Biggins, D.E., and Alldredge, W., 2003, Basal metabolism of the black-footed ferret (*Mustela nigripes*) and the Siberian polecat (*M. eversmannii*): Journal of Mammalogy, v. 84, p. 497–504.

Hillman, C.N., 1968, Field observations of black-footed ferrets in South Dakota: Transactions of the North American Wildlife and Natural Resources Conference, v. 33, p. 433–443.

Hillman, C.N., and Linder, R.L., 1973, The black-footed ferret, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 10–20.

Hillman, C.N., Linder, R.L., and Dahlgren, R.B., 1979, Prairie dog distributions in areas inhabited by black-footed ferrets: American Midland Naturalist, v. 102, p. 185–187.

Houston, B.R., Clark, T.W., and Minta, S., 1986, Habitat suitability index model for the black-footed ferret—a method to locate transplant sites: Great Basin Naturalist Memoirs No. 8, p. 99–114.

Joyce, S.L., 1988, Feeding behavior and water requirements of black-footed ferrets (*Mustela nigripes*): Laramie, University of Wyoming, M.S. thesis, 82 p.

King, C., 1990, The natural history of weasels and stoats: Ithaca, N.Y., Cornell University Press, 253 p.

Lehmer, E.M., and Biggins, D.E., 2005, Variations in torpor patterns of free-ranging black-tailed and Utah prairie dogs across gradients of elevation: Journal of Mammalogy, v. 86, p. 15–21.

Leopold, A., 1933, Game management: New York, Charles Scribner’s Sons, 481 p.

Linder, R.L., Dahlgren, R.B., and Hillman, C.N., 1972, Black-footed ferret–prairie dog interrelationships, *in* Symposium on rare and endangered wildlife of the Southwestern United States: Santa Fe, New Mexico Department of Game and Fish, p. 22–37.

Miller, B.J., Menkens, G.E., and Anderson, S.H., 1988, A field habitat model of black-footed ferrets, *in* Eighth Great Plains Wildlife Damage Control Workshop Proceedings: U.S. Department of Agriculture, Forest Service, General Technical Report RM-154, p. 98–102.

Paunovich, R., and Forrest, S.C., 1987, Activity of a wild black-footed ferret litter: Prairie Naturalist, v. 19, p. 159–162.

Pearl, R., and Reed, L.J., 1920, On the rate of growth of the population of the United States since 1790 and its mathematical representation: Proceedings of the National Academy of Sciences, v. 6, p. 275–288.

Powell, R.A., 1979, Mustelid spacing patterns—variations on a theme by *Mustela*: Zeitschrift für Tierpsychology, v. 50, p. 153–165.

Powell, R.A., Clark, T.W., Richardson, L., and Forrest, S.C., 1985, Black-footed ferret (*Mustela nigripes*) energy expenditure and prey requirements: Biological Conservation, v. 34, p. 1–15.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming (USA): American Midland Naturalist, v. 117, p. 225–239.

Severson, K.E., and Plumb, G.E., 1998, Comparison of methods to estimate population densities of black-tailed prairie dogs: Wildlife Society Bulletin, v. 26, p. 859–866.

Sheets, R.G., Linder, R.L., and Dahlgren, R.B., 1972, Food habits of two litters of black-footed ferrets in South Dakota: American Midland Naturalist, v. 87, p. 249–251.

Stromberg, M.R., Rayburn, R.L., and Clark, T.W., 1983, Black-footed ferret energy requirements—an energy balance estimate: Journal of Wildlife Management, v. 47, p. 67–73.

Section V. Reestablishing Populations

Reintroduction of black-footed ferrets was a primary focus of attention during the decade of the 1990s. This phase of recovery was envisioned in the 1988 recovery plan to encompass experiments with rearing of ferrets, development of monitoring techniques, testing of release methods, and further investigations of black-footed ferret ecology. Experiments with rearing and release of ferrets have been conducted. Improved rearing methods and prerelease conditioning have dramatically enhanced postrelease survival of ferrets, and a new captive breeding center was designed to accommodate those methods. Other data from many ferret releases have been evaluated to produce the papers of this section.

Monitoring Black-footed Ferrets During Reestablishment of Free-ranging Populations: Discussion of Alternative Methods and Recommended Minimum Standards

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Abstract

Although the monitoring of black-footed ferret (*Mustela nigripes*) populations following reintroductions has not been haphazard, several ferret recovery groups since 1994 have recommended development of uniform standards prescribing minimum methods, intensities, and frequencies of monitoring that would provide data on population size, mortality rates, and recruitment. Such standards would promote comparability of data among sites, document expectations for those who will attempt to establish new populations, and allow the U.S. Fish and Wildlife Service and other responsible groups to better assess progress made toward achieving recovery objectives. Our recommendations are based on methods that have been successfully used to monitor natural and reintroduced populations of ferrets and are an attempt to balance needs and costs. We suggest a combination of marking ferrets with passive integrated transponder (PIT) tags and annual spotlight searches coupled with automated transponder readers to individually identify survivors. Unmarked ferrets should be captured and implanted with PIT tags whenever possible. These and other methods are detailed. Circumstances that may dictate other methods or more intensive monitoring (e.g., high rates of loss or low recruitment) also are discussed.

Keywords: anesthesia, black-footed ferret, monitor, *Mustela nigripes*, snow tracking, spotlight, transponder, trap

Introduction

The need to prescribe standards for monitoring black-footed ferrets (*Mustela nigripes*) at reintroduction sites has become apparent to the U.S. Fish and Wildlife Service (FWS) and members of the Black-footed Ferret Interstate Coordinating Committee (ICC), who discussed formulating standards at the ICC annual meetings of 1994 and 1995. That need was reaffirmed as an action item in an American Zoo and Aquarium Association program review (Hutchins and others, 1996) and at the Black-footed Ferret Conservation Subcommittee (of the Black-footed Ferret Recovery Implementation Team) meeting of 2001. Standards are needed in order to (1) accurately assess progress toward recovery goals, (2) clearly define monitoring expectations for future sites for black-footed ferret reintroduction, (3) provide guidance regarding methods and associated limitations, (4) assure FWS that participants provide consistent feedback on progress, and (5) make limited data comparable for broad-scale interpretations.

The need for standards does not imply that monitoring is presently haphazard. Indeed, several groups releasing black-footed ferrets have used similar strategies, most commonly spotlighting, to evaluate ferret status and trends; however, standardizing would increase the opportunity for comparisons among sites, years, and other variables of interest. Our suggestions are an attempt to balance needs and cost. Our goal was to prescribe methods that maximize applicability of the most basic data but would not preclude any group from participation because of cost. Reviews of monitoring efforts during the early years of ferret reintroductions in Wyoming, Montana, South Dakota, Arizona, Utah, Colorado, and Mexico revealed strengths and weaknesses that influenced our recommendations. This prescription defines minimum levels of monitoring, but we encourage all working groups to consider using more intensive monitoring efforts, when applicable, to help address questions of importance to recovery goals.

We are not suggesting procedures for so-called clearances (U.S. Fish and Wildlife Service, 1988) related to section 7 of the Endangered Species Act, although some of the techniques we discuss are useful for those purposes. We do not exhaustively analyze or describe methods beyond the minimum

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prescription (e.g., radio telemetry) but provide references for more information on those topics. We describe monitoring of black-footed ferrets only; monitoring of prairie dog populations, associated species, and diseases at reintroduction sites is also important, but such topics are beyond the scope of this paper.

Objectives

To monitor is to watch, observe, or check, especially for a real purpose (*Webster's New Collegiate Dictionary*). Monitoring is needed to accomplish the following objectives:

- assess progress toward site-specific population establishment and make attendant decisions related to the need to continue to release captive-bred animals and numbers that should be released,
- detect serious problems or catastrophic population declines (e.g., due to diseases) that might be remediated,
- assess recovery at the national level, and
- test hypotheses regarding methods involved in establishing self-sustaining ferret populations (e.g., rearing, release, translocation, disease prevention, ferret searches, predation reduction).

Specifically, monitoring may provide data to (1) estimate population size, composition, and rates of natality and mortality; (2) assess genetic representation within a population; (3) identify causes of mortality; (4) document spatial distribution of ferrets including dispersal and habitat use; and (5) assess condition of ferrets, exposure to diseases, and parasite loads.

Types of Data: Balancing Needs and Costs

Useful minimum monitoring levels must produce information that identifies whether or not there are serious problems and allows assessment of progress toward local and national recovery goals (the first three objectives listed above). If losses of ferrets are low during initial releases, and if later populations appear to be self-sustaining, then monitoring can be maintained at these minimum levels. If problems are evident (e.g., excessive losses of ferrets), then we suggest increased levels of monitoring to identify their causes. The alternatives are site abandonment or sustained augmentation of ferrets. Abandonment does not contribute to our understanding and may result in repeated mistakes. Sustained augmentation seems inefficient but may, in the end, be needed at some sites.

The fourth listed objective of monitoring relates to experimentation and hypothesis testing to better understand the ecology of ferrets and improve reintroduction strategies, thereby enhancing the prospect for successful species recovery. This objective may necessitate monitoring that is different and sometimes more intensive than the minimum levels prescribed below. This learning objective is sufficiently important to programmatic decisions that it may at times take precedence over other objectives. Needs vary by site and year; further discussion of this objective is beyond the scope of this paper.

Minimum data needed to accomplish the first three objectives are estimates of population size, survival rates, and annual recruitment. A critical review of the last four decades of black-footed ferret monitoring, however, reveals that there never have been estimates of these attributes that were free of known biases. Recently, we have qualified these estimates as “minimums,” recognizing that not all ferrets will be found (Biggins and others, 1998). Moreover, “survival” rates should really be termed “retention” rates, where failure to retain ferrets at a reintroduction site can be due to emigration or mortality. Retention rates are likely biased downward because of undetected ferrets, but actual survival rates could be higher than retention rates if dispersal away from the reintroduction sites occurred without concurrent mortality. Population size, survival, recruitment, and associated variances can be estimated with closed form models or iterative numerical optimization if unbiased surveys are repeated over short time spans (Otis and others, 1978; White and others, 1982), and even more analytical tools are available if those multiple surveys done in short spans are replicated again over longer spans (robust designs: Kendall and others, 1995; Hines and others, 2003; program MARK: White and Burnham, 1999). The increased effort in repeated surveys is obvious, but avoiding bias caused by observer familiarity gained during previous surveys calls for additional constraints, problematic logistics, and even greater costs. Thus, we believe that the effort required could not be sustained over multiple reintroduction sites and years; the 24-year history of rather intensive monitoring of black-footed ferrets provides ample evidence regarding how much can be accomplished with available resources. Realistically, the tactics that have been used over the past 10 years are likely to remain the ones used to monitor black-footed ferret populations in the future, and the measures of population size, survival, and recruitment obtained by those monitoring methods (described below) will have to serve as indices to population attributes.

Although those indices (e.g., population size) are biased, they are nearly always based on complete coverage of respective reintroduction sites during spotlight surveys. Thus, issues of spatial sampling are not relevant. Although coverage may be complete, the counts are not a census because all ferrets are not found. We do not regard this bias as a fatal flaw, in part because it is unlikely to be large and in part because the counts can be adjusted for effort, providing indices that are particularly useful in a comparative sense (e.g., comparisons among groups and years within sites). Diminishing cumulative detections of unique ferrets over several days of spotlight searches (discussed below) provide reassuring evidence that large numbers of ferrets usually do not remain undetected during spotlight surveys. The standardization of search methods suggested below also will enhance comparability of data sets.

Data Collection Methods

Relatively few techniques have proven effective to “watch, observe, and check” black-footed ferrets; each method has its advantages, disadvantages, limitations, and risks. The methods currently used are snow tracking, spotlighting, capture-mark-recapture, and radio telemetry, but each can be utilized at varying levels of intensity and can be coupled with other strategies to increase the quality and quantity of data. Indeed, use of multiple methods allows cross-checking and verification of data.

Snow Tracking

Snow tracking involves searching from the ground or aircraft to locate tracks and other sign (especially diggings) of black-footed ferrets. Individual ferrets can sometimes be identified based on geographic location of tracks and origin and terminus points. Counts can be cumulative, giving an estimate of ferret numbers, provided that snow conditions remain optimal for at least several days. The strategy involves searching along ground transects (Richardson and others, 1987) or aerial flight lines (Biggins and Engeman, 1986; Miller and Biggins, 1988) until tracks or diggings are encountered. Track sets then are individually followed from origin to terminus to determine individuality and gather accessory information on movement pattern (use of space, but only crudely related to time) and to opportunistically collect scat for diet information. Broad-scale searches for tracks have revealed the presence of ferrets on prairie dog colonies that would not otherwise have been monitored. Absence of tracks, however, does not prove absence of ferrets because ferrets may remain inactive for many days following a snowstorm.

Snow tracking is least likely to adversely impact ferrets, requires little specialized equipment, and is relatively inexpensive. The principal disadvantage is weather dependency; although snow is common in the northern and western portion of the ferret’s original range, good tracking conditions occur only sporadically. Best results are attained when snow cover is continuous and undisturbed for several days. Warm sunny spells can cause patchiness, and winds can quickly erase evidence. Prairie dog (*Cynomys* spp.) tracks cause confusion during searches from the air and ground and may obliterate ferret tracks; however, white-tailed prairie dogs (*C. leucurus*) and Gunnison’s prairie dogs (*C. gunnisoni*) routinely hibernate, and black-tailed prairie dogs (*C. ludovicianus*) also may enter torpor (Lehmer and others, 2001), allowing effective midwinter ferret searches during prolonged spells of calm, cold weather following accumulations of snow. A team of searchers must respond immediately when favorable conditions develop. Each site should have a snow-tracking plan targeting priority areas for searches so that implementation can be rapid and efficient. Identification of mustelid tracks is not always straightforward; long-tailed weasel (*Mustela frenata*) tracks cause potential confusion (Miller and Biggins, 1988). Individual identities of ferrets can be ascertained if they have been marked with passive integrated transponder (PIT) tags (see subsection on Capture, Handling, and Marking). If ferrets are not individually identified, conservative time and space separation criteria should be used (see subsection on Minimum Level of Monitoring) to determine the minimum number of different ferrets present because ferrets can move long distances each night and because several ferrets can reside in close proximity.

Spotlighting

Spotlighting has been the universal technique for finding black-footed ferrets (Campbell and others, 1985). Prairie dog colonies are scanned at night with high-intensity spotlights by individuals on foot or in vehicles (e.g., all-terrain vehicles or trucks). Recently, most spotlighting has been conducted by using continuous illumination while the observer moves slowly (10 km/h), but earlier workers, searching on relatively small prairie dog colonies, preferred a systematic schedule of intermittent illumination from a fixed location (Henderson and others, 1969; Fortenbery, 1972). Standardization to the extent possible is very important because variation in the manner of implementation can lead to erratic results, but standardization must be balanced with site-specific needs.

Compared to snow tracking, spotlighting gives much more accurate temporal data to accompany spatial data. The eyes of ferrets reflect an emerald green shine, but other animals, such as badgers (*Taxidea taxus*), coyotes (*Canis latrans*), weasels (*Mustela* spp.), deer (*Odocoileus* spp.), and pronghorns (*Antilocapra americana*), can cause confusion. Interorbital distance, distance from ground, and behaviors help distinguish ferrets from some other mammals, but distances can be deceiving at night, and experience is necessary for reliable and efficient identification. Coyotes tend to briefly look at the spotlight, run a short distance, stop, and then look at the spotlight again. Weasels dart about much more quickly than ferrets and have a more subdued eyeshine. Swift foxes (*Vulpes velox*) run with a rigid gait, so the eyeshine does not undulate, then may stop and briefly lay close to the ground. When ferrets are moving, their eyeshine tends to bounce because of their bounding gait. Deer and pronghorns have much larger eyes and tend to be bedded down at night in groups; their eyeshine rises when they stand up.

Reported detection rates range from 1.4–102.6 hours per black-footed ferret sighting and up to nearly 264 hours per unique ferret located (table 1) for surveys of reintroduced and wild populations. Sighting rates are influenced by ferret density, but topography, vegetation, and varying behaviors of the animals (e.g., because of weather, season, origin of stock, rearing method) may also contribute to variation in sightability

Table 1. Examples of search efforts expended for locating black-footed ferrets (*Mustela nigripes*) with spotlights.

Location	Time	Source	Hours	Number of hours/ ferret sighting	Number of hours/unique ferret sighting
Southwest South Dakota	1966–67	Hillman (1968)	462.0	4.0	
Meeteetse, Wyo.	Summer 1983	Forrest and others (1988)	260.0		3.0
	Summer 1984	Forrest and others (1988)	554.0		4.3
	Summer 1985	Forrest and others (1988)	647.0		11.2
Shirley Basin, Wyo.	October 1991	Hnilicka and Luce (1992)	121.5		12.2
	November 1991	Hnilicka and Luce (1992)	258.5		28.7
	Summer 1992	Hnilicka and Luce (1993)	1,256.1	35.9	125.6
	November 1992	Hnilicka and Luce (1993)	925.1	17.5	51.4
	Summer 1993	Luce and others (1994)	675.8		35.6
	October 1993	Luce and others (1994)	1,244.7		52.0
	Summer 1994	Staley and Luce (1995)	570.7		95.1
	October 1994	Staley and Luce (1995)	591.3	34.8	118.3
C.M. Russell NWR, Mont.	1994–96	Stoneberg (1996)	952.7	3.1	5.9
Conata Basin/Badlands, S. Dak.	Fall 1994	Plumb and Marinari (1996)	247.5	7.7	35.4
	Summer 1995	Plumb and Marinari (1996)	600.4	26.1	66.7
Conata Basin, S. Dak.	September 16–23, 2002	T. Livieri (unpub. data)	462.0	1.4	3.1
Aubrey Valley, Ariz.	June–December 2002	Winstead and others (2003)	1,847.0	102.6	263.9
Aubrey Valley, Ariz.	June–November 2003	Hoss and others (2004)	2,014.0	69.4	83.9

(Marinari, 1992). The probability of detecting an individual free-ranging ferret with spotlights has not been estimated for any set of conditions. Cumulative counts over time, however, have been plotted and may generically illustrate probability of detection during short time spans, assuming no mortality occurs. Data from the Meeteetse, Wyo., population of ferrets on white-tailed prairie dog habitat suggest that about 82 percent of the cumulative total number of ferrets had been counted after four nights of spotlight searches (Forrest and others, 1988). Similar data from spotlighting in 17 black-tailed prairie dog colonies in the Conata Basin of South Dakota (T. Livieri, unpub. data, 2002) resulted in a steeper curve, with 92 percent of the cumulative total counted after three nights and 98.5 percent counted after four nights (fig. 1). For the South Dakota data set, the cumulative proportion of ferrets counted also increased as a function of cumulative time spent spotlighting adjusted by area covered during the search (fig. 2). Although most ferrets appear to be found during diligent searches, individuals can be elusive. In Utah, a female remained undetected for 24 months (three surveys) (B. Zwetzig, oral commun., 2004); in Arizona, two females were not located for 27 months (Hoss and others, 2004); and an adult male in South Dakota was first relocated 40 months after release (W. Perry, oral commun., 1998).

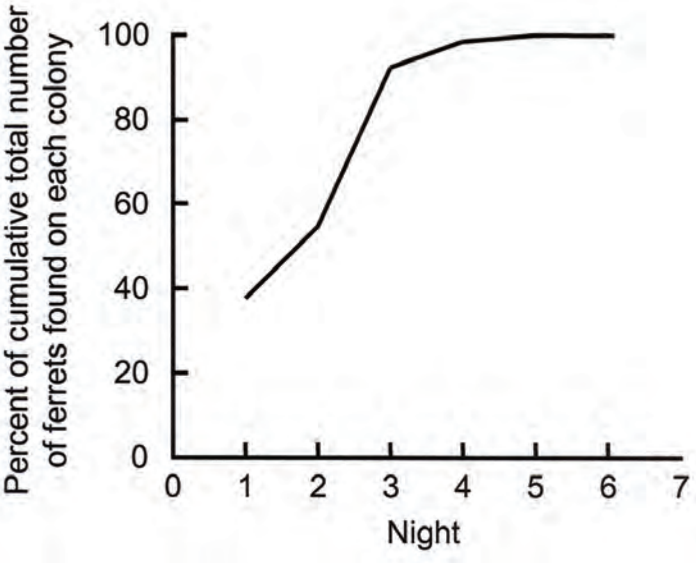

Figure 1. Black-footed ferrets (*Mustela nigripes*) encountered per night during spotlight searches on 17 black-tailed prairie dog (*Cynomys ludovicianus*) colonies, September 16-22, 2002, in Conata Basin, S. Dak.

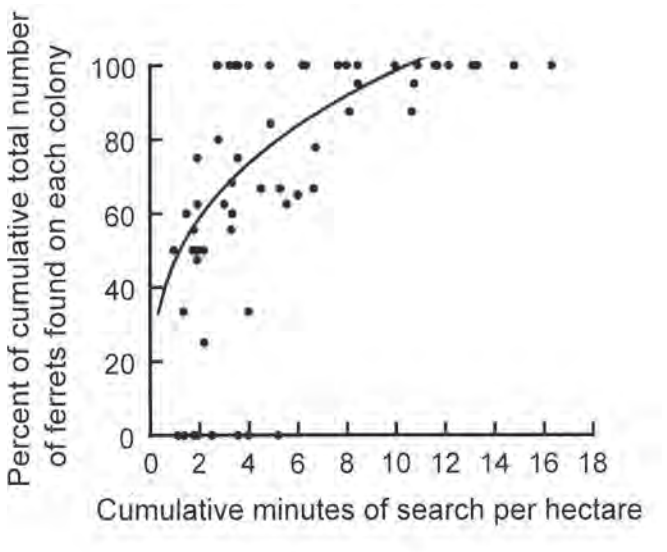

Figure 2. Black-footed ferrets (*Mustela nigripes*) encountered per minute per hectare during spotlight searches on 17 black-tailed prairie dog (*Cynomys ludovicianus*) colonies, September 16-22, 2002, in Conata Basin, S. Dak. An exponential curve was fitted to data.

Table 2. Percent of the cumulative total number of black-footed ferrets (*Mustela nigripes*) counted during 1999–2002 at Conata Basin, S. Dak.

	Cumulative counts				
	1999	**2000**	**2001**	**2002**	**Mean**
			Males		
July–August	71.4	70.0	85.2	65.4	73.0
September	92.9	76.7	92.6	96.2	89.6
October	92.9	93.3	100.0	100.0	96.6
November	100.0	96.7	100.0	100.0	99.2
December–on	100.0	100.0	100.0	100.0	100.0
			Females		
July–August	93.9	92.9	88.3	94.1	92.3
September	100.0	100.0	95.0	100.0	98.8
October	100.0	100.0	100.0	100.0	100.0
November	100.0	100.0	100.0	100.0	100.0
December–on	100.0	100.0	100.0	100.0	100.0

Cumulative total spotlight counts of ferrets continue to increase over time spans of months, but in these longer spans it is not reasonable to assume that the estimates are unaffected by losses of animals. For a 4-year data set from South Dakota (T. Livieri, unpub. data, 1999–2002; data from those colonies that were repeatedly searched each month), monthly detection rates for males appeared to be lower than rates for females (table 2). Assuming a constant monthly survival rate of 0.9763 (annual survival of 75 percent), the increasing cumulative monthly counts in table 2 can be approximated by (constant) monthly spotlight detection rates of 0.722 for males and 0.918 for females. These estimates need refinement but seem to reflect differences in ability to detect adult males and adult females with spotlight searches.

Spotlighting can alter behaviors of black-footed ferrets. Responses to the lights seem to vary among individual ferrets. Some ferrets may avoid the light by decreasing aboveground activity, and others may attempt to escape through increased movements (Campbell and others, 1985). Spotlights emitting white light probably should not be used for prolonged observations of a ferret (Campbell and others, 1985). More equipment (e.g., spotlights, backpack units, batteries) is needed for spotlighting than for snow tracking. Similar to snow tracking, located ferrets can be identified with remote transponder readers or through capture.

Capture, Handling, and Marking

Whether ferrets are located by spotlighting or snow tracking, identification of each individual may enable (1) cumulative minimum counts of animals while positively avoiding double counting, (2) an overview of dispersal movements, (3) tests of hypotheses regarding comparisons between treatments (e.g., rearing conditions, sex, site, habitat use, release method; Biggins and others, 1998), and (4) assessment of likely matrilineal relationships within populations (Biggins and Godbey, 2003). With some monitoring designs, marking also may allow (1) use of mark-recapture methods for population estimation (Otis and others, 1978; White and others, 1982; White and Burnham, 1999; Rivest and Daigle, 2004), (2) use of survival estimators (Lebreton and others, 1992), and (3) estimation of age-specific mortality rates.

Successful methods for marking ferrets are passive integrated transponder (PIT) implants (Fagerstone and Johns, 1987) and ear tattoos (Fagerstone and others, 1985). Tattoos are usually identifiable only on ferrets that are in hand and sometimes become illegible or disappear entirely. Less commonly, transponders have ceased functioning or have been lost from the ferrets. Passive integrated transponder tags are relatively inexpensive and easy to install and have become the preferred technique for marking ferrets. Two transponders should be implanted, one on the posterior part of the head and the second dorsally between the hips. After a ferret has been located by spotlighting or snow tracking, its transponders can be identified with an automated reader that is left at the occupied burrow (Stoneberg, 1996) (fig. 3), or the ferret can be captured and identified with a hand-held reader.

If an attempt at automated transponder reading fails, capture can be used as a backup. Capture involves additional stress on animals (Thorne and others, 1985) but provides an

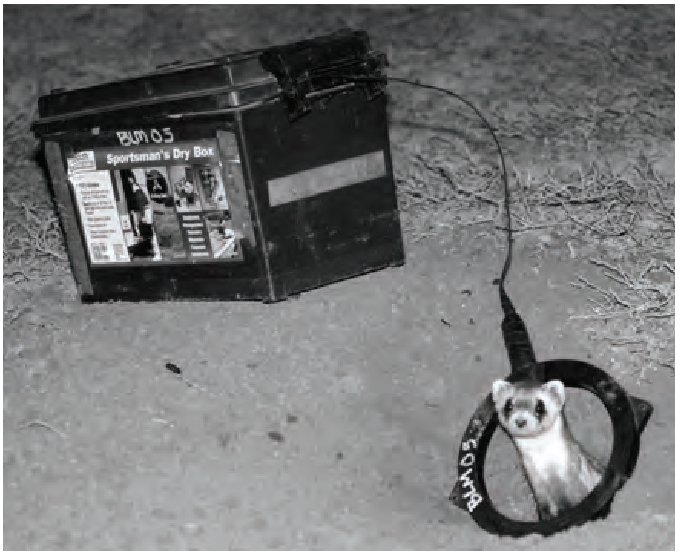

Figure 3. Automated passive integrated transponder readers in waterproof boxes may be left at burrows occupied by black-footed ferrets (*Mustela nigripes*). Transponder numbers will be recorded as the ferret passes near (or through) the loop antenna placed to encircle the burrow entrance.

opportunity to assess condition and take samples of blood, parasites, etc. These samples could prove invaluable in disease evaluations and for genetic studies. Traps (see fig. A1 in appendix) must be in good working order. It is exasperating to find a malfunctioning trap at the end of an extended attempt to capture an animal. If a burrow system is thought to have multiple openings, openings lacking traps may be plugged with rocks, wood, or plastic cups (44 oz). When trapping is finished, all traps must be retrieved, and all burrows must be unplugged.

Dye marking captured ferrets can prevent double counting during a survey and helps identify ferrets already captured during a trapping session. Dye can be applied to captured animals without use of anesthetics. Effective dyes include Nyanzol D (Hoogland, 1995) and hair dyes. Dyes, however, are temporary compared to transponders, lasting at best until the next molt; PIT tags should be used whenever possible, whether or not fur is dyed.

Anesthesia is necessary for many of the procedures mentioned above. Anesthetics used in the field on black-footed ferrets have included ketamine, a ketamine-medetomidine mixture (reversed with atipamezole) (Kreeger and others, 1998), telazol, and isoflurane. Gas anesthesia (including isoflurane) requires a relatively bulky and complicated apparatus, including an induction chamber, vaporizer, mask, oxygen bottle, and connecting tubes. Isoflurane, however, allows a highly controllable level of anesthesia and maintenance of much higher blood oxygen concentrations (Gaynor and others, 1997).

Field technicians who need to capture and handle black-footed ferrets must complete a certification course. Presence of a veterinarian is beneficial when using anesthetics and handling ferrets. Ferrets should not be released until fully recovered from anesthesia, which may take hours with some injectable anesthetics.

Radio Telemetry

Radio telemetry has been used on black-footed ferrets since 1981 (Biggins and others, 1985, 1986). Telemetry has distinct advantages; animals are individually identifiable from remote locations with minimal human disturbance, behaviors can be monitored remotely (e.g., movements, home ranges, activity cycles, dispersal), fates can be identified, additional methods of survival analysis are available (Heisey and Fuller, 1985; Pollock and others, 1989), causes of mortality can be identified, and habitat use can be objectively assessed (White and Garrott, 1990). Disadvantages include the expense and impact of placing transmitter packages on or in the animals. Ferrets are assumed to be influenced by a transmitter, whether external or implanted; the effect can vary from trivial to devastating. Discussions about whether or not to use radio telemetry should focus on the degree of suspected impact weighed against potential gains in knowledge. Neck abrasions have been caused by collars, and premature collar loss has been common. The currently recommended collar is made of wool and degrades within several weeks to months (Biggins, Godbey, Miller, and Hanebury, this volume).

Compared to spotlighting and snow tracking, radio telemetry on black-footed ferrets is expensive and relatively difficult to master. Use of radio triangulation during ferret reintroductions has concentrated on intensive but short-term (30–60 days postrelease) data collection to compare behaviors of animals and document their fates (Biggins and others, 1999: Biggins, Godbey, Livieri, and others, this volume). Less labor-intensive, automated signal detection was used in releases of ferrets in South Dakota and Montana with emphasis on determining fates of ferrets, but interpretation of data was problematic. Because of the large commitment of time and funds and the possibility of adverse impacts on ferrets carrying transmitters, we regard radio telemetry as a specialized tool that should not be considered for routine monitoring of black-footed ferrets (Biggins, Godbey, Miller, and Hanebury, this volume).

Alternative Techniques

Other techniques that have been used in attempts to locate ferrets include scent dogs (Reindl, 2004); scent attractants coupled with remote cameras or transponder readers; implantable radio transmitters; long-range transponders; night vision equipment, such as light amplifiers and infrared detectors; and track plates. To date, these techniques have not proved widely applicable under field conditions, but they may become more useful in the future.

Recommended Standards

Minimum Level of Monitoring

Under the present circumstances and state of technology, we recommend marking all ferrets, including as many wild-born individuals as possible, with two transponder chips; spotlighting to locate black-footed ferrets; and identifying all ferrets located by using combinations of remote transponder readers and capture. Dye marking in addition to PIT tagging can allow the searchers to bypass ferrets, avoiding the need to set a reader or capture the animals to find out if they have already been PIT tagged. Failure to read the PIT tag each time a ferret is located, however, may preclude more rigorous assessments of population attributes and ferret movements. Exactly how these tools are deployed depends on the phase of reintroduction and the objectives for monitoring.

For sites where ferrets are released in fall, we recommend a minimum of two spotlighting periods, the first beginning 30 days after the final release (if there were several, closely spaced, sequential releases) and the second, postreproductive survey beginning in August of the following year. An existing ferret population that has not received additional releases of ferrets during the previous 12 months may be monitored with an August survey only. A prebreeding survey in March–April is highly desirable (for both recently released and established populations) but is not considered a requirement. If possible, ferret searches should be conducted during bright moonlight. Preliminary analyses for Siberian polecats (*M. eversmannii*) and black-footed ferrets suggest that radio-tagged individuals of both species were more active during bright nights (full moon) than during dark nights (new moon); when the moon was partially illuminated, they were more active during the part of the night when moonlight was present than when it was absent (Biggins, 2000).

Clark and others (1984) suggested methods for locating ferrets, and the FWS later recommended criteria for black-footed ferret surveys to clear prairie dog towns for development activities, application of toxicants, or other actions that might be detrimental to an existing population of black-footed ferrets (U.S. Fish and Wildlife Service, 1988). Because the guidelines were developed from techniques used at Meeteetse to monitor a wild population, some aspects are applicable to the standards proposed here for monitoring released ferrets. The basic recommendations of the survey guidelines are reiterated below, and each of these is followed by suggested modifications (if any) applicable to the minimum standards for monitoring reintroduced ferret populations.

1. When monitoring existing populations, surveys should be conducted between August 1 and September 30. This is the period when young ferrets have become sufficiently active above ground that they can be captured for marking, and it is normally prior to dispersal so that litters are usually separately identifiable. Adult males seem to be less detectable than adult females during this period (table 2).

2. Prairie dog towns should be continuously surveyed between dusk and dawn on each of three to five consecutive nights to ensure systematic coverage and increased opportunity to discover black-footed ferrets. A ferret can stay inactive for days (Biggins and others, 1986; Richardson and others, 1987), presumably depending on weather and its food supply. We suggest adding more nights (if necessary) until no (or few) new ferrets are found. If scheduling dictates that spotlighting cannot be continuous from dusk until dawn, then gaps in coverage should be rotated among nights so that no time period is neglected.

3. Detection depends on the ferret being above ground and facing the observer at the time the spotlight is directed toward it. Pass the spotlight across the landscape, and follow with a sweep back across the same path. A ferret looking away from the light during the first pass may become curious and turn toward the light on the second pass. Large prairie dog towns should be divided into tracts, and each tract should be systematically and repeatedly searched. Each searcher should concentrate on an area that ensures at least one pass every 30–60 minutes. Rough terrain, dense vegetation, and lack of road access may dictate small tracts to result in effective coverage. On occasion, the objective may be only to document presence or absence of ferrets on colonies, in which case tracts could be large (up to 800 ha). The area should be as small as practical to increase the opportunity for detection. In some cases backpack spotlighting may be necessary (e.g., if vehicle access is impossible or legally restricted). If searches are done on foot, then each person should concentrate on about 130 ha or less. Boundaries of tracts should be well marked to keep searchers oriented at night.

4. Observations on each prairie dog town or tract searched should begin at a different geographic point on each successive night to maximize the chance of intercepting a black-footed ferret during its nighttime activities, the patterns of which tend to be somewhat animal specific and repetitive. Even within a night, searchers should consider varying their search patterns while ensuring even coverage (e.g., alternate traveling north-south and east-west).

5. Previous guidelines suggested that survey crews consist of one vehicle and two observers equipped with two spotlights of 200,000–300,000 candle power. Teams searching for ferrets in areas with known populations have used a wider variety of equipment and organizational strategies. Single searchers on foot, in trucks, and with all-terrain vehicles (ATVs) have been effective, and other types of spotlight equipment also have been used. Because relative efficiency of various strategies is somewhat site dependent, we propose no limits. Use equipment that is suitable for the weather, terrain, and personnel.

Additional specifications include the following:

1. It is better to search each site entirely within a short time span by using a large number of searchers than to use few people over a long time span. The long-span, low-intensity method leads to problems in specifying the time interval for which the estimate is relevant (e.g., for estimating survival) and increases potential for confusion in counting individuals that are not recaptured or otherwise identified (e.g., double counting or missing ferrets that moved).

2. Use a systematic sampling scheme giving uniform coverage to the entire area, even though higher densities of burrows may be present in some areas than others. Resist the temptation to repeatedly return to places where ferrets have been seen. Some of the fringe areas of prairie dog colonies may have the largest populations of prairie dogs, and intuitive perceptions of habitat quality are not always reliable. Provide markers to assist with relocating ferrets and orienting the surveyor.

3. Diligently attempt to identify all ferrets. If a transponder cannot be read remotely, then try to capture the ferret. If some members of the team are more adept at capture than others, then consider using them as a dedicated "capture" crew whose job is to capture and identify ferrets rather than search for them. Occasionally, individual ferrets can be identified by unique physical characteristics that can be distinguished after capture or, even more uncommonly, without capture. Acceptable examples we have seen include deep scars, missing portions of ears, and missing toes. We do not consider differences in coloration and individual mask patterns to be sufficiently reliable for individual identification.

4. If individual ferrets are not identifiable, then we recommend a conservative approach to classifying them as separate individuals. Unless snow allows absolute separation of track sets, ferrets can be classified as separate individuals only if it was nearly impossible for an animal to have moved between the two locations during the time interval between sightings. For sightings separated by <500 m, the sightings must be simultaneous (fig. 4). For sightings separated by longer distances, we assumed a maximum speed of 6 km/h for a ferret, decreasing in a nonlinear manner with increasing distance. This maximum has been used to screen radio-telemetry data for errors (Breck and Biggins, 1997). We reduced the maximum speed to a low of 0.694 km/h with a separation of 50 km because the maximum documented movement of a ferret in a 3-day period was about 50 km (Biggins and others, 1999). Two sightings with distance and time separations that plot above the curves of figure 4 can be assumed to be separate individuals. This approach mandates substantial evidence for inclusion of animals into a population count. To avoid underestimation of population size for unmarked populations, a larger survey crew will be

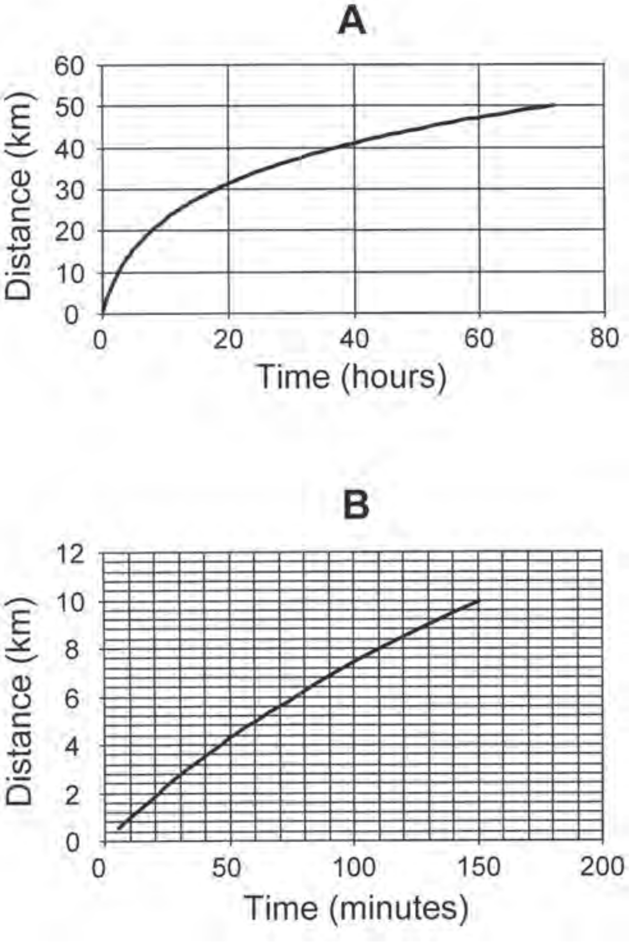

Figure 4. Minimum separations of distance and time needed to classify two sightings of black-footed ferrets (*Mustela nigripes*) as different individuals. Plot B is the lower portion of the curve in plot A, rescaled to provide better resolution. Separations of two sightings plotting above the curves can be considered separate individuals (e.g., two sightings 4 km apart separated by 30 minutes).

necessary (to increase the probability of simultaneous sightings of ferrets living in close proximity to each other).

5. A brief meeting should occur the morning following each spotlight search session to discuss results from the previous night. One important purpose is to assess the number of unique individuals that are likely represented by ferrets seen but not identified (using the criteria of 4 immediately above).

6. Use a standardized form with a map on the reverse side. Record all nonspotlighting periods (e.g., rest breaks) on the form, sketch ferret locations on the map, and place a marked flag at each ferret location. Use Global Positioning System (GPS) equipment to obtain coordinates of ferret locations, and record these coordinates on the data form (see appendix for examples of forms and checklists). Once coordinates and other necessary data have been collected, remove all flags.

7. Ferrets should be double marked before release with two PIT tags (anterior and posterior). At present, incompatibility among manufacturers requires that the ferret program adopt a single system. The tags and readers currently used in the ferret program are made by AVID® Microchip I.D. Systems (Folsom, La.). Transponder technology is developing rapidly, and other systems may be practical in the future.

8. Unmarked ferrets that are wild caught should be marked or re-marked if they have lost previous markings. Field anesthesia by a veterinarian or certified individual is necessary.

9. An annual report to the FWS should include a table listing all ferrets identified in monitoring surveys. Ideally, the table should be in a commonly used computer spreadsheet. For each ferret, the following accessory information should be provided:
   a. Studbook number and field identification number (telemetry number, site-specific wild-born animal number, PIT tag number, etc.)
   b. Sex
   c. Method of identification
   d. Date(s) of capture or identification
   e. Location(s) of capture or identification (Universal Transverse Mercator [UTM] coordinates from GPS receiver; include datum and grid zone)
   f. Observer(s)
   g. Date of original release (if applicable)
   h. Specimens taken (blood, fecal, parasites, etc.)
   i. Other data taken (weight, measurements, etc.)
   j. If previously unmarked wild-born kit, identify litter size and associated dam.

10. A standard release form (see appendix), filled out for each ferret released, should also be forwarded to the Black-footed Ferret Recovery Program Coordinator. As in 9 above, the forms can be tabulated and forwarded in spreadsheet form on a magnetic disk (see Plumb and Marinari [1996] for an example table).

Recommended Precautions—Legality, Human Safety, and Animal Safety

1. If using all-terrain vehicles (ATVs), heavy batteries used to power spotlights can change weight distribution and make the vehicles unstable.

2. Riders of ATVs should be certified if required by the employer. Night operation and use of a spotlight increase the difficulty. Special training should be provided on ATV safety and night use. Use appropriate protective gear and clothing.

3. Obtain all permits and notify appropriate authorities regarding timing and location of spotlighting activity. Spotlighting is prohibited or regulated in some States. A Federal endangered species permit will be required.

4. Listen to weather reports and be familiar with local conditions. Weather can change rapidly, and impending changes may not be obvious at night. Hazards include lightning, dangerously large hail, tornadoes, and disorientation at night, especially in snowstorms. These phenomena are not imaginary; spotlight searchers have had close calls with all of them.

5. Searchers should be fully familiar with their assigned areas, which may require a visit during daylight. A compass or personal GPS unit may allow a technician to avoid becoming lost during thick fog or heavy snowfall. Searchers should work in pairs when there is a threat of adverse weather.

6. The survey crew should be as well equipped as possible with two-way radios. For safety and efficiency, it is especially important to maintain frequent communication with individuals working in remote areas.

7. Landowners must agree (preferably in writing) to the activities being conducted on or around their properties and should be kept well informed of progress.

8. Respect property, whether public or private. Avoid rutting muddy roads, and follow applicable rules and procedures for off-road driving with ATVs or larger vehicles. If you inadvertently damage property (e.g., gates, fences, cattle guards), make any needed repairs or arrange to have them done.

9. Spotlights are disruptive, so minimize the observation time with intense white light. After locating a ferret, it should be observed in the periphery of the light beam, using the least illumination possible to maintain contact for necessary follow-up activities (e.g., transponder reading, trapping). Avoid repeated harassment of the same animal.

10. When trapping, do not separate a mother from her kits for extended periods. Although unusual circumstances may dictate either more lenient or more restrictive limits, we suggest limiting such separations to <24 hours during late July–September. Separations should be much shorter if it becomes necessary to trap an adult female (that has young kits) earlier in the season. Remember that a burrow blocked by a trap can separate the dam from her kits even if no ferrets are caught. Traps should be checked at least once per hour by approaching the trap and looking all the way into it. Closed traps should not be left in burrows (ferrets have been inadvertently caught in closed traps). Badgers and other predators can kill an entrapped ferret, and severe weather can cause hyperthermia or hypothermia.

11. Use properly maintained traps. Traps that are poorly maintained or misused have injured ferrets. For example, ferrets have received abrasions and lacerations when forcing their way through gaps at the back door, even though the doors were secured with clips. We recommend clipping or otherwise fastening each corner of the back door. Check for treadle sensitivity, protruding wires, broken welds, and bent parts. Poorly maintained traps may increase the amount of time spent harassing an animal if repeated attempts become necessary to catch it. Wrapping traps in pieces of wool blanket or burlap helps protect a captured ferret from wind and cold and seems to create a more enticing tunnel that may facilitate capture and keep the animal calm after capture.

12. Ferrets usually should be released into the burrow where they were captured and during hours of darkness whenever possible. If necessary, a ferret may be held in a cool location until the following night. A portion of a prairie dog can be given to any ferret that must be captured for handling or marking to help mitigate the stress of the procedure. If presented at the time of release, ferrets often will take these offerings into the burrow. Prairie dog remains may attract badgers or other predators, so their use should be judicious and closely monitored. If your site is within the known range of plague, we suggest precautions to avoid inadvertently feeding plague-contaminated carcasses (use prairie dogs from plague-free zones or those that have been properly quarantined).

13. Contact the Black-footed Ferret Recovery Program Coordinator for latest developments regarding trapping and handling ferrets, and refer to Thorne and others (1985) for additional details.

The best training for monitoring black-footed ferrets is assisting in an effort that is already underway. Persons who will be responsible for monitoring at a new reintroduction site should participate in monitoring at an existing site well before the new project begins.

Expanding Beyond the Minimum Standards

1. Groups of ferrets may be released sequentially at a site throughout extended periods (60 days or more). Spotlight surveys have been conducted 30 days after the last release (Montana and South Dakota) and 30 days after the midpoint of extended releases (Wyoming). For releases over relatively long spans of time, a solution might be to conduct more than 1 survey at about 30 days postrelease, treating groups of animals as separate releases.

2. Prior estimates of survival of released ferrets using spotlighting data were treated as minimum survival because ferrets may have remained undetected during surveys. With several searches repeated over a short time span (e.g., 2 weeks) true survival rate or population size may be estimable. Separate estimates of the probability of detection and accompanying variation could be investigated with repeated sampling within short time spans. The assumption of no emigration or other losses is problematic, so each complete search should be carried out quickly (one to three nights) and repeated as often as expedient.

3. As conditions permit, snow tracking should be used to augment spotlighting. Data collected by snow tracking may not be directly comparable to spotlighting data. Because maximum comparability through standardization across sites and years is an important consideration, snow tracking may supplement spotlighting but cannot replace it. Ferret scats have been collected during snow tracking, providing additional opportunities for evaluations of food habits (Sheets and others, 1972; Campbell and others, 1987) and for molecular genetic assessments.

4. Telemetric monitoring will most likely provide con-

structive feedback for management decisions if used during the first release at a new site, at sites with high rates of ferret disappearance, during a dramatic population decline, or in studies designed to test hypotheses having wide-scale implications (see also Biggins, Godbey, Miller, and Hanebury, this volume). In the interest of avoiding additional burden to a dwindling population, it may be tempting to reduce monitoring intensity (and eliminate telemetry) at a time when information is most desperately needed. The information gained through detailed studies during a crisis may be critically important for future success at that site and for the recovery program in general. A "failure" may be recharacterized as a success if enough is learned to avoid repetition of the event at that same site or at other sites. As with snow tracking, use of radio telemetry does not eliminate the need for the spotlight surveys.

5. The addition of a spring spotlighting survey, conducted as described above for the fall and summer surveys, provides a useful assessment of overwinter survival and an estimate of the breeding population of ferrets. These surveys are often conducted in March or April (Matchett, 1997).

Other Issues—Duration of Monitoring Program, Altering the Intensity, Monitoring and Research

If the ferret population is not yet near estimated carrying capacity but its growth is as expected or above, the minimum monitoring strategy should be adequate. Because there will be a need to know when a population may require augmentation, and when a population is doing so well that it can be a source of animals for other populations, annual monitoring at these minimum levels should be conducted for each year that ferrets are released and at least 2 years following the final release. A ferret population may be surveyed in alternate years if it has a positive growth rate or remains stable because of birth of kits at the site for 2 years following the final release and if the site will not be serving as a source for translocations of ferrets. The most intensive monitoring should be planned for the first few years of releases at a site when there are many questions and no established record of success, with decreases in intensity during subsequent years. If population growth becomes slow or negative, intensive monitoring again is appropriate to identify the problem(s). Increased spotlighting and/or radio telemetry may be needed in some cases. Other types of monitoring (e.g., for diseases such as plague and distemper; prairie dog abundance and habitat quality) are also needed, and their results help define the relative need for ferret monitoring. The situation predictably will be dynamic, calling for flexibility in program management. If some working groups have insufficient resources to respond rapidly to changes, the leadership in the national program may need to recommend reallocation of resources (e.g., funds authorized under section 6 of the Endangered Species Act, different priorities for research support) to sites in response to shifting needs. Even the minimum monitoring standards proposed above may need modification if (1) the entire program becomes dramatically more or less successful than at present, (2) funding radically changes, (3) available habitat becomes fully occupied by ferrets, and (4) new technology makes more efficient techniques available. We strongly recommend close communication between working groups and national program managers during the process of formulating site-specific monitoring plans.

The suite of methods described for monitoring black-footed ferrets has been used for both research and management applications, but the distinction between the two purposes is poorly defined. Many ferret releases in the near future probably will have a blend of learning objectives (implying research with indirect benefits to long-term recovery) and population establishment objectives (implying management actions with direct, short-term benefits). A single monitoring program often contributes to both purposes. For example, snow tracking in 1982–86 at Meeteetse yielded winter population estimates for ferrets, helping to track the welfare of the population in the immediate sense, and gave information on movements of animals and other aspects of ecology (Richardson and others, 1987). Used during releases of ferrets, radio telemetry has allowed relocation of animals that dispersed into unsuitable habitat and has enabled documentation of heavy losses of ferrets to predation, information with important short-term management implications. In several cases, the primary purpose of radio telemetry was to test hypotheses of differential survival and behavior of groups of ferrets produced and released under varying conditions (Biggins and others, 1999). The minimum spotlighting standards recommended above emphasize the immediate need to assess population attributes. Addressing other objectives probably will require a more intensive strategy, expanded by adding other methods and/or increasing the amount of spotlighting (spatially or temporally).

References Cited

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., and Engeman, R.M., 1986, Aerial survey for black-footed ferret sign in snow, *in* Abstracts of contributed papers, 13th International Biometric Conference, Seattle, Wash.: Washington, D.C., International Biometric Society, p. 7.2.

Biggins, D.E., and Godbey, J.L., 2003, Challenges to reestablishment of free-ranging populations of black-footed ferrets: Comptes Rendus Biologies, v. 326, p. S104–S111.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Schroeder, M., Forrest, S., and Richardson, L., 1985, Movements and habitat relationships of radio-tagged black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 11.1–11.17.

Biggins, D.E., Schroeder, M.H., Forrest, S.C., and Richardson, L., 1986, Activity of radio-tagged black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 135–140.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Breck, S.W., and Biggins, D.E., 1997, Detecting and eliminating errors in radio-telemetry data sets—a comparison of screened and unscreened data [abs.], *in* Forum on wildlife telemetry—innovations, evaluations, and research needs: Jamestown, N. Dak., Northern Prairie Wildlife Research Center, U.S. Geological Survey, p. 15.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Campbell, T.M., III, Clark, T.W., Richardson, L., Forrest, S.C., and Houston, B.R., 1987, Food habits of Wyoming black-footed ferrets: American Midland Naturalist, v. 117, p. 208–210.

Clark, T.W., Campbell, T.M., III, Schroeder, M.H., and Richardson, L., 1984, Handbook of methods for locating black-footed ferrets: Cheyenne, Wyoming BLM Technical Bulletin No. 1, 55 p.

Fagerstone, K.A., Biggins, D.E., and Campbell, T.M., III, 1985, Marking and radiotagging of black-footed ferrets (*Mustela nigripes*), *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 10.1–10.10.

Fagerstone, K.A., and Johns, B.E., 1987, Transponders as permanent identification markers for domestic ferrets, black-footed ferrets, and other wildlife: Journal of Wildlife Management, v. 51, p. 294–297.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Fortenbery, D.K., 1972, Characteristics of the black-footed ferret: U.S. Fish and Wildlife Service, Resource Publication 109, 8 p.

Gaynor, J.S., Wimsatt, J., Mallinckrodt, C., and Biggins, D., 1997, A comparison of sevoflurane and isoflurane for short-term anesthesia in polecats: Journal of Zoo and Wildlife Medicine, v. 28, p. 274–279.

Heisey, D.M., and Fuller, T.K., 1985, Evaluation of survival and cause-specific mortality rates using telemetry data: Journal of Wildlife Management, v. 49, p. 668–674.

Henderson, F.R., Springer, P.F., and Adrian, R., 1969, The black-footed ferret in South Dakota: South Dakota Department of Game, Fish and Parks, Technical Bulletin 4, 37 p.

Hillman, C.N., 1968, Life history and ecology of the black-footed ferret in the wild: Brookings, South Dakota State University, M.S. thesis, 28 p.

Hines, J.E., Kendall, W.L., and Nichols, J.D., 2003, On the use of the robust design with transient capture-recapture models: Auk, v. 120, p. 1151–1158.

Hnilicka, P., and Luce, B., 1992, Post-release surveys of free-ranging black-footed ferrets in Shirley Basin during fall and winter of 1991–1992, *in* Oakleaf, B., Luce, B., Thorne, E.T., and Torbit, S., eds., 1991 annual completion report, black-footed ferret reintroduction, Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, p. 172–195.

Hnilicka, P., and Luce, B., 1993, Spotlighting and snowtracking surveys for free-ranging black-footed ferrets from 13 July 1992–11 January 1993 in Shirley Basin, Wyoming, *in* Oakleaf, B., Luce, B., Thorne, E.T., and Williams, B., eds., 1992 annual completion report, black-footed ferret reintroduction, Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, p. 158–187.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing mammal: Chicago, University of Chicago Press, 557 p.

Hoss, K.A., Volz, T.A., Smith, L.R., Hackl, C.Z., Goodman, S.J., and Van Pelt, W.E., 2004, Results of the 2003 black-footed ferret release effort in Aubrey Valley, Arizona: Phoenix, Arizona Game and Fish Department, Nongame and Endangered Wildlife Program Technical Report, 20 p.

Hutchins, M., Wiese, R.J., and Bowdoin, J., 1996, Black-footed ferret recovery program analysis and action plan: Bethesda, Md., American Zoo and Aquarium Association, 137 p.

Kendall, W.L., Pollock, K.H., and Brownie, C., 1995, A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design: Biometrics, v. 51, p. 293–308.

Kreeger, T.J., Vargas, A., Plumb, G.E., and Thorne, E.T., 1998, Ketamine-medetomidine or isoflurane immobilization of black-footed ferrets: Journal of Wildlife Management, v. 62, p. 654–662.

Lebreton, J.D., Burnham, K.P., Clobert, J., and Anderson, D.R., 1992, Modeling survival and testing biological hypotheses using marked animals—a unified approach with case studies: Ecological Monographs, v. 62, p. 67–118.

Lehmer, E.M., Van Horne, B., Kulbartz, B., and Florant, G.L., 2001, Facultative torpor in free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*): Journal of Mammalogy, v. 82, p. 552–557.

Luce, B., Hunter, L., and Oakleaf, B., 1994, Spotlighting and snowtracking surveys for free-ranging black-footed ferrets from 25 July–30 November 1993 in Shirley Basin, Wyoming, *in* Luce, B., Oakleaf, B., Thorne, E.T., and Williams, E.S., eds., 1993 annual completion report, black-footed ferret reintroduction, Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, p. 63–96.

Marinari, P.E., 1992, Detectability of black-footed ferrets (*Mustela nigripes*) using spotlighting: Laramie, University of Wyoming, M.S. thesis, 123 p.

Matchett, R., 1997, Annual report of black-footed ferret recovery activities, UL Bend and Charles M. Russell National Wildlife Refuges, southern Phillips County, Montana: Lewistown, Mont., U.S. Fish and Wildlife Service, 71 p.

Miller, B.J., and Biggins, D.E., 1988, Winter monitoring of black-footed ferrets (*Mustela nigripes*): Fort Collins, Colo., U.S. Fish and Wildlife Service, 17 p.

Otis, D.L., Burnham, K.P., White, G.C., and Anderson, D.R., 1978, Statistical inference from capture data on closed animal populations: Wildlife Monographs 62, 135 p.

Plumb, G.E., and Marinari, P.E., 1996, Black-footed ferret monitoring in Badlands National Park, September 1994–September 1995, *in* McDonald, P.M., Marinari, P.E., and Plumb, G.E., eds., Black-footed ferret reintroduction: year one completion report, Conata Basin, Badlands, South Dakota: Wall, S. Dak., U.S. Forest Service, p. 94–115.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., and Curtis, P.D., 1989, Survival analysis in telemetry studies—the staggered entry design: Journal of Wildlife Management, v. 53, p. 7–15.

Reindl, S.A., 2004, Efficacy of scent dogs in detecting black-footed ferrets (*Mustela nigripes*) at a reintroduction site in South Dakota: Brookings, South Dakota State University, M.S. thesis, 60 p.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming: American Midland Naturalist, v. 117, p. 225–239.

Rivest, L.P., and Daigle, G., 2004, Loglinear models for the robust design in mark-recapture experiments: Biometrics, v. 60, p. 100–107.

Sheets, R.G., 1972, A trap for capturing black-footed ferrets: American Midland Naturalist, v. 88, p. 461–462.

Sheets, R.G., Linder, R.L., and Dahlgren, R.B., 1972, Food habits of two litters of black-footed ferrets in South Dakota: American Midland Naturalist, v. 87, p. 249–251.

Staley, G., and Luce, B., 1995, Spotlighting and snowtracking surveys for free-ranging black-footed ferrets from 25 July 1994–15 February 1995 in Shirley Basin, Wyoming, *in* Luce, B., Oakleaf, B., Thorne, E.T., and Williams, E.S., eds., 1994 annual completion report, black-footed ferret reintroduction, Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, p. 34–69.

Stoneberg, R., 1996, Implanted microchips used to individually identify black-footed ferrets in Montana: Prairie Naturalist, v. 28, p. 163–168.

Thorne, E.T., Schroeder, M.H., Forrest, S.C., Campbell, T.M., III, Richardson, L., Biggins, D., Hanebury, L.R., Belitsky, D., and Williams, E.S., 1985, Capture, immobilization and care of black-footed ferrets for research, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 9.1–9.8.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

White, G.C., Anderson, D.R., Burnham, K.P., and Otis, D.L., 1982, Capture-recapture and removal methods for sampling closed populations: Los Alamos, N. Mex., Los Alamos National Laboratory, 235 p.

White, G.C., and Burnham, K.P., 1999, Program MARK—survival estimation from populations of marked animals: Bird Study, v. 46 (suppl.), p. 120–138.

White, G.C., and Garrott, R.A., 1990, Analysis of wildlife radio-tracking data: San Diego, Calif., Academic Press, 383 p.

Winstead, R.A., Hoss, K.A., Volz, T.A., Hooge, J., Smith, L., and Van Pelt, W.E., 2003, Results of the 2002 black-footed ferret release effort in Aubrey Valley, Arizona: Phoenix, Arizona Game and Fish Department, Nongame and Endangered Wildlife Program Technical Report, 26 p.

Appendix. Forms, Checklists, and Other Information that May Be Useful When Spotlighting, Capturing, and Handling Black-footed Ferrets

Spotlight Schedule/Assignments

Night of: ______________________________

Hours: ______________________________

Name	PDTs/route	Vehicle	No. of readers	Radio	Missing BFF/other

Black-footed Ferret (BFF) Survey Form

Mark sequential observation numbers on reverse-side map. Flag each location with BFF ID, date, and time for later GPS mapping.

Observer: ______________________ Night of: ______________________
(e.g., 3/19–20/98)

Transportation type: ______________________

Prairie dog colony: (Sketch area searched on map on reverse side.)

Cloud cover: ______________________ Moon phase: ______________________

Snow cover %: ____________ Temp.: ________ Wind speed/direction: ____________

Comments: ____

____

Start and end time	Map and observation number	Time seen	BFF ID	Transponder number	Location	Time trap set/checked	Predators observed

Total search minutes: ____________

Black-footed Ferret Markings

ID	Sex	Date	Head transponder	Pelvis transponder	Dye	Location	CDV

Black-footed Ferret Handling Checklist

1. __________Verify lack of transponder, other markings, and need to handle

2. __________Date ________Time ________ Sex ________ Age ________ ID

3. __________Dam ________ Stud ________ Location and plot on map

4. __________Trapper ________ Team

5. __________Anesthetize at 3.0–4.0 ISO ________ Time

6. __________DIAL ISOFLURANE TO 1.75, transfer to face mask ________ Time

7. __________PATIENT NO.

Time	ISO	Oxygen	Pulse rate	% oxygen saturation	Respiration rate	Temperature

8. __________ Implant transponder chips HEAD ______________ PELVIS ______________
9. __________ Test transponder chips
10. __________ Collect hair and label envelope
11. __________ Collect blood and label VACUTAINER (cc) __________ NOBUTO (y/n) _______
12. __________ Give 1 cc, SC canine distemper vaccine. If recapture, booster given at 2 weeks
13. __________ Give penicillin injection (<1,000 g = 0.3 mL SC| >1,000 g = 0.4 mL SC)
14. __________ Apply dye mark: ADULT MALE = ---- WILD MALE = X OTHER
    ADULT FEMALE = | WILD FEMALE = 0
15. __________ Health inspection notes, read old tattoo, teeth, anomalies, etc.

16. __________ ISOFLURANE AND OXYGEN OFF
17. __________ Weigh
18. __________ Monitor recovery
19. __________ Disinfect/clean all equipment and surfaces, prepare for next animal

Dosages of Injectable Anesthetics for Black-footed Ferrets

KETAMINE/DIAZEPAM DOSAGES
premixed 10 mL KET (1,000 mg) with
2 mL DIAZEPAM (10 mg)

MEDETOMIDINE/KETAMINE
3.0 mg/kg KETAMINE + 0.075 mg/kg MEDETOMIDINE
Antagonize with 0.45 mg/kg; ATIPAMEZOLE after ≥30 min

Weight (g)	Light (20 mg/kg; cc)	Medium (25 mg/kg; cc)	T/T dose (30 mg/kg; cc)	Heavy (35 mg/kg; cc)	KET (cc)	MED (cc)	TOT (cc)	ATI (cc)
100	0.020	0.025	0.030	0.035	0.075	0.038	0.11	0.045
200	0.040	0.050	0.060	0.070	0.150	0.075	0.23	0.090
300	0.060	0.075	0.090	0.105	0.225	0.113	0.34	0.135
400	0.080	0.100	0.120	0.140	0.300	0.150	0.45	0.180
500	0.100	0.125	0.150	0.175	0.375	0.188	0.56	0.225
600	0.120	0.150	0.180	0.210	0.450	0.225	0.68	0.270
700	0.140	0.175	0.210	0.245	0.525	0.262	0.79	0.315
800	0.160	0.200	0.240	0.280	0.600	0.300	0.90	0.360
900	0.180	0.225	0.270	0.315	0.675	0.338	1.01	0.405
1,000	0.200	0.250	0.300	0.350	0.750	0.375	1.13	0.450
1,100	0.220	0.275	0.330	0.385	0.825	0.412	1.24	0.495
1,200	0.240	0.300	0.360	0.420	0.900	0.450	1.35	0.540
1,300	0.260	0.325	0.390	0.455	0.975	0.488	1.46	0.585
1,400	0.280	0.350	0.420	0.490	1.050	0.525	1.58	0.630
1,500	0.300	0.375	0.450	0.525	1.125	0.562	1.69	0.675

$$\text{DOSAGE} = \frac{\text{BODY WEIGHT * DOSE}}{\text{CONCENTRATION}}$$

MED/KET CONCENTRATIONS: KET = 4.0 mg/mL
MED = 0.2 mg/mL
ATI = 1.0 mg/mL

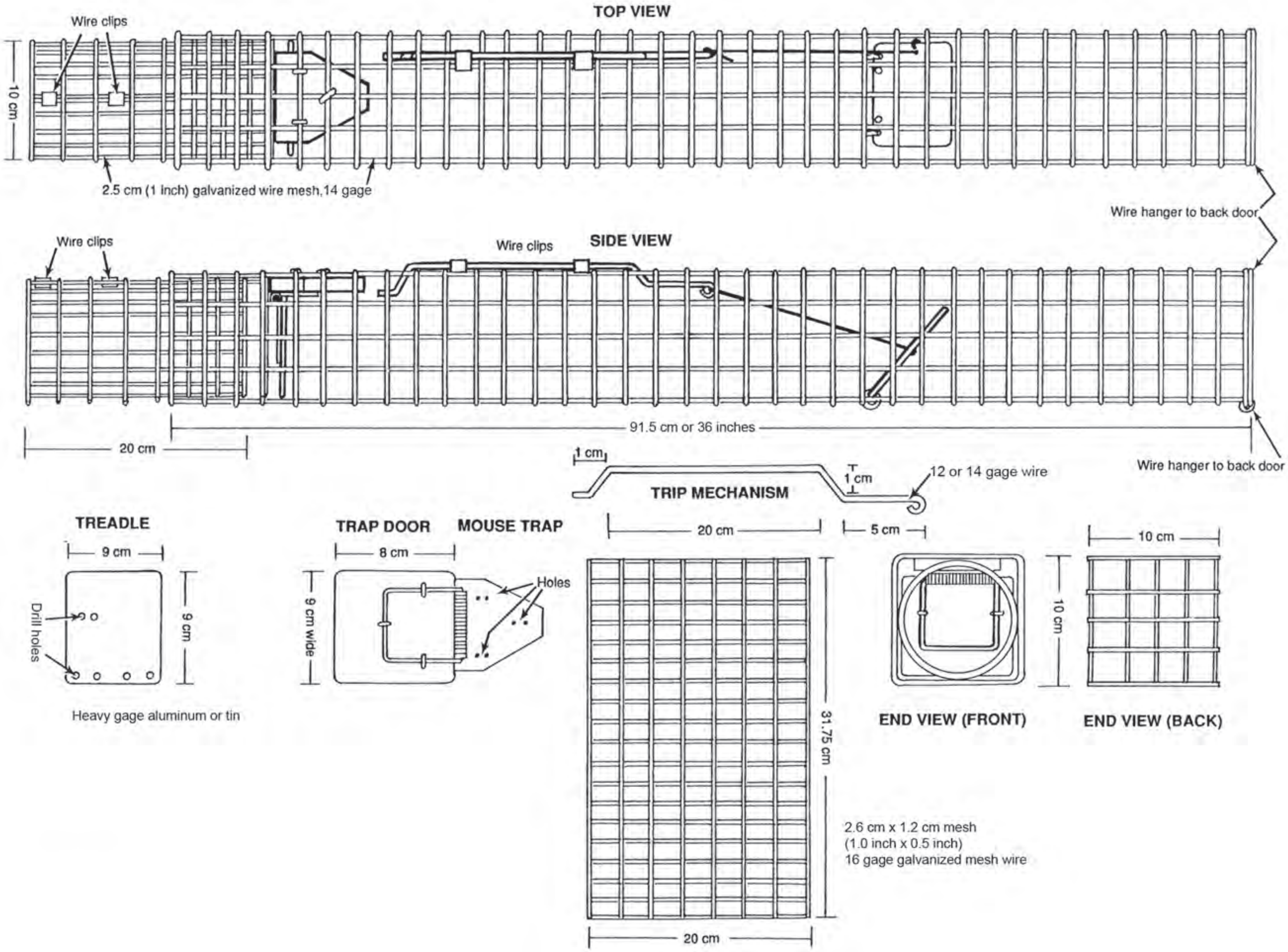

Figure A1. Design of a trap for black-footed ferrets (*Mustela nigripes*). This trap is a modification of the model described by Sheets (1972).

Radio Telemetry for Black-footed Ferret Research and Monitoring

By Dean E. Biggins,[1] Jerry L. Godbey,[1] Brian J. Miller,[2] and Louis R. Hanebury[3]

Abstract

By 1973, radio telemetry was regarded as an important potential tool for studying the elusive, nocturnal, and semifossorial black-footed ferret (*Mustela nigripes*), but fears of using invasive techniques on this highly endangered mammal caused delays. We began radio collaring ferrets in 1981. Use of radio telemetry on ferrets proved to be both challenging and rewarding. We document two decades of development and use that led to the present radio-tagging techniques and methods for radio tracking. The 7-g radio collar commonly used after 1992 was smaller and lighter, relative to mass and size of subjects, than collars used in studies of other *Mustela*. Other important developments were a Teflon® coating to shed mud, a highly flexible stainless steel cable for whip antennas, and a nondurable wool collar. Although collar-caused neck abrasions have continued to occur sporadically, a retrospective assessment of minimum survival rates for 724 reintroduced ferrets (392 radio tagged), using data from spotlight surveys, failed to detect negative effects of radio-collars. In a South Dakota study, ferrets that were found to have hair loss or neck abrasions when collars were removed did not exhibit movements significantly different from those of radio-tagged ferrets with no evidence of neck problems. Prototype transmitters designed for surgical implantation had insufficient power output for effective use on ferrets. Early attempts at tracking radio-tagged ferrets by following the signal on foot quickly gave way to following movements by triangulation, which does not disturb the subjects. The most effective tracking stations were camper trailers fitted with rotatable, 11-element, dual-beam Yagi antennas on 6-m masts. We used radio telemetry to produce 83,275 lines of data (44,191 indications of status and 39,084 positional fixes via triangulation) for 340 radio-collared ferrets during the reintroduction program. Tracking by hand and from aircraft augmented triangulation, allowing us to locate animals that dispersed long distances and enabling us to determine causes of mortality. Justifying further use of radio telemetry on black-footed ferrets requires careful consideration of costs and benefits.

Key words: black-footed ferret, collar, *Mustela eversmannii*, *Mustela nigripes*, radio telemetry, radio tracking, Siberian polecat, survival, triangulation

Introduction

Radio telemetry has been used as a tool to study vertebrates for more than 50 years (Kimmich, 1979) and *Mustela* since the mid-1970s (Erlinge, 1979). The technique is especially useful for re-locating individual animals that are highly mobile, secretive, and difficult to observe. Black-footed ferrets (*M. nigripes*) are among the most nocturnal of carnivores, and they are semifossorial, attributes that reduce our ability to monitor them with other techniques. Ferrets may be located with spotlights, a technique that is often employed for conducting annual surveys of their abundance (Campbell and others, 1985; Biggins and others, 1998a). Spotlighting, however, affects the behaviors of ferrets (Campbell and others, 1985), making it less attractive for the intensive monitoring that may be required for behavioral studies. Techniques must be matched to objectives, and the relative advantages and disadvantages of radio telemetry, spotlighting, and snow tracking for studying black-footed ferrets have been summarized elsewhere (Biggins, Godbey, Matchett, and others, this volume). This article addresses the challenges of applying radio telemetry to studies of black-footed ferrets, in part to help a potential investigator decide whether it is the appropriate tool for the goals of the project being considered.

Because of difficulties encountered by earlier researchers in studying this secretive species and because technologies were rapidly advancing, radio telemetry was recognized as a “vital” tool for future ferret investigations (commentary by E. Brigham in Linder and Hillman, 1973, p. 162). Erickson (1973, p. 156) emphasized a need to use radio telemetry on ferrets, lamenting that “the black-footed ferret is one of the least well known of all of the endangered mammals of the United States, despite 10 years of intensive research.” The anticipated importance of this tool was reflected in a primary objective of the first captive breeding program for

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black-footed ferrets (commencing in 1971), which was “not to produce animals for release in the wild, but to learn more about . . . safe marking methods” and “means of following their travels and home range” (commentary by R. Erickson in Linder and Hillman, 1973, p. 26). These experiences of the 1970s motivated development of prototype transmitters for black-footed ferrets, but, by the latter years of that decade, no free-ranging ferrets could be found. Our use of radio telemetry on black-footed ferrets began in 1981 with the discovery of the last known extant population west of Meeteetse, Wyo. Our intent is to review the use of radio telemetry for black-footed ferret research during the subsequent two decades. There is a particular need to document the problems and our attempts to find solutions. Detailed discussions of hardware and methods that did not work seem as important as discussion of the triumphs, if only to provide a better starting point for those who might wish to engage in improving the techniques. We review the challenges of radio tagging these animals, methods used to gather data once they have been tagged, and methods for analyzing those data.

Radio Tagging Black-footed Ferrets

In a prophetic prediction of upcoming problems, Erickson (1973, p. 157) stated “There is no known way to safely develop and test methods of installing radio-transmitter harnesses on live ferrets in the wild.” Although the first transmitter packages intended for use on black-footed ferrets (fig. 1) were indeed tested on surrogate domestic ferrets (*M. putorius furo*; fig. 2) (C. Hillman and S. Martin, oral commun., 1980), problems developed when the collars were first used on black-footed ferrets at Meeteetse in 1981–82. Neck abrasions sometimes occurred with these 15-g collars, and they had low power output (table 1, version A-1), in part caused by the inefficient brass loop antenna that also served as a collar (fig. 1). The low power resulted in frequent loss of contact with subjects (Fagerstone and Biggins, 1986). Although a more powerful collar prototype was produced in 1982 (table 1, version B-1), it seemed too bulky for use on ferrets. That transmitter was attached to a harness, but tests on surrogate prairie dogs (*Cynomys* spp.) (fig. 3) were unsuccessful. The original packages were again used in 1982, but the brass loop collars were difficult to fit and collar loss was high (Fagerstone and Biggins, 1986). These first radio collars for ferrets transmitted on 164 MHz.

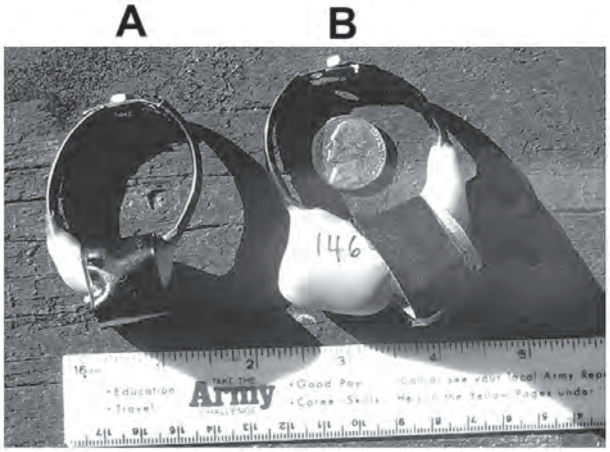

Figure 1. The first radio collars tested for use on black-footed ferrets (*Mustela nigripes*), ca. 1979 (version A-1 of table 1). A model similar to “A” was used on ferrets. Photograph by D. Biggins.

Figure 2. Early transmitter packages with tuned loop antennas (version A-1 of table 1) were tested on domestic ferrets (*Mustela putorius furo*). Photograph by U.S. Fish and Wildlife Service.

We also conducted comparative experiments with reception of signals emanating from underground transmitters on 30 MHz and 164 MHz, reasoning that the longer wavelengths would better penetrate soil. The lower frequencies performed no better than the higher frequencies during underground trials, but problems with transmitting and receiving antennas were exacerbated with the lower frequencies (lower frequencies need larger antennas for efficient transmission and reception). All subsequent transmitters were on 164–165 MHz at frequencies licensed to the U.S. Department of the Interior.

Early in 1983 we submitted specifications for a new transmitter collar to manufacturers of wildlife telemetry equipment, requesting their assistance in producing an improved transmitter package. Prototypes from three of the five companies that responded exceeded dimensional or weight limits. Two units (table 1, version D-1, fig. 4; table 1, version C-1, fig. 5) seemed satisfactory and were used on 10 black-footed ferrets in August 1983 (Fagerstone and Biggins, 1986). Reception range was several times greater with model D-1 than with model A-1 used in 1981–82. During 1983, however, breakage of the whip antenna was common, and sometimes accumulations of clay resulted in large increases in mass and dimensions of the transmitter package (fig. 6). The accumulations of clay likely were partially responsible for some neck injuries. Various treatments and coatings, including polished acrylic (fig. 7A), wool (fig. 7B), and Teflon® (DuPont, Wilmington, Del.) heat-shrink tubing (fig. 8), were used in laboratory trials and on prairie dogs and ferrets in the field during 1983 and 1984 to alleviate the mud accumulation problem (Fagerstone and Biggins, 1986). The Teflon tubing solved the problem of mud accumulation; however, its slippery surface seemed to

Table 1. Transmitter packages tested during development of radio-telemetry applications for black-footed ferrets (*Mustela nigripes*).

Version	Year	Type	Weight (g)	Antenna	Effective power[1]	Pulse		Battery life (days)
						Width[2]	Rate[3]	
A-1	1981	collar	15	14.0-cm loop	-35		104	100
B-1	1982	harness		44.5-cm whip	-9	14	34	
C-1	1983	collar	10	8.9-cm whip	-35	104	30	39
D-1	1983	collar	13	15.2-cm whip	-12	25	66	
E-1	1983	collar		16.5-cm whip	-40		19	
D-2	1989	collar	10	15.2-cm whip	-18	11–40	25–67	59+
A-2	1991	collar	9	20.3-cm whip			variable	variable
D-3	1992	collar	7	20.3-cm whip	-20	25	47	50
D-4	1985	implant	18	internal coil	-41		47	
D-5	1985	implant	4	whip	-37		80	
E-2	1985	implant	26	internal coil	-39		60	

[1] Decibels relative to 1 milliwatt (dBm).
[2] Milliseconds duration.
[3] Pulses per minute.

Figure 3. Capsules with high power output (Telonics, Inc., Mesa, Ariz.) (version B-1 of table 1) were attached to harnesses and tested on surrogate prairie dogs (*Cynomys* spp.) in 1982. Photograph by D. Biggins.

Figure 5. A package coated with soft plastic used on black-footed ferrets (*Mustela nigripes*) in 1983 (version C-1 of table 1). Photograph by D. Biggins.

Figure 4. A 13-g transmitter package (version D-1 of table 1) used on black-footed ferrets (*Mustela nigripes*) during 1983–84. Photograph by D. Biggins.

exacerbate collar loss, and there were several instances of neck abrasions.

Continued problems with collar loss in 1984 motivated additional investigation and development of transmitter attachment methods for ferrets. Disease outbreaks in Meeteetse prairie dogs and ferrets (Forrest and others, 1988; Ubico and others, 1988) ended all hope for continued research on that free-ranging population of ferrets; however, the ensuing captive breeding program and its ultimate goal of reintroductions underscored the importance of improving radio telemetry for ferrets. In trials conducted in the spring of 1985, two of three free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*) developed neck sores when fitted with old-style ferret collars made of vinyl-impregnated cloth but did not seem adversely affected by neckbands of wool ($n = 4$) or leather ($n = 4$). Prairie dogs gained 40 percent in mass during a 3-month period. Wool collars sewed with cotton thread often wore sufficiently to be lost by prairie dogs in 3 to 6 months. Thus, a black-footed ferret with a wool

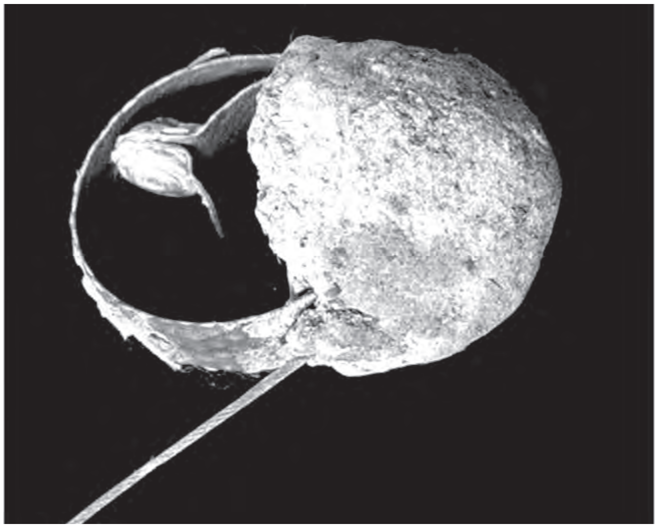

Figure 6. A collar from 1983 that accumulated a large buildup of clay while carried by a black-footed ferret (*Mustela nigripes*). Photograph by D. Biggins.

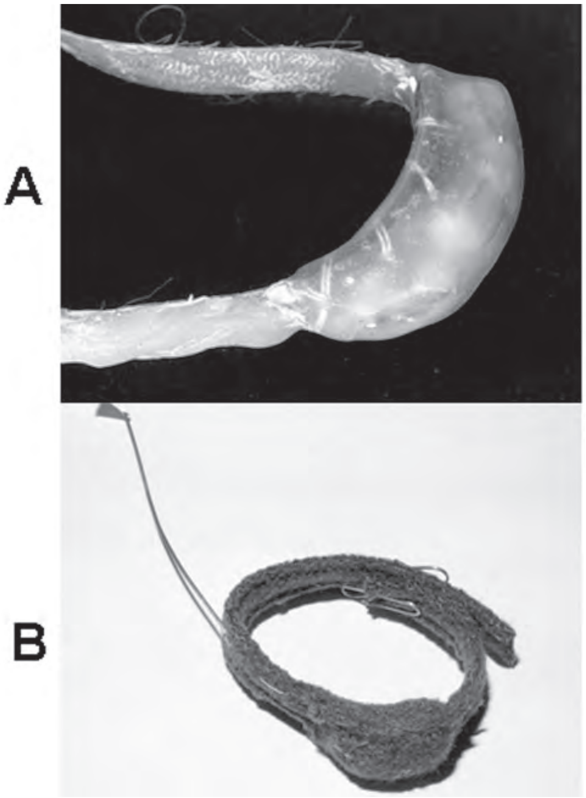

Figure 7. The acrylic potting material was polished (A) or encased in wool (B) in attempts to alleviate mud accumulation. Photograph by D. Biggins.

neckband would not be collared permanently if its radio failed prematurely and the animal could not be relocated for collar removal.

One of the goals of research initiated in 1988 on Siberian polecats (*Mustela eversmannii*) and other surrogate species was to advance our proficiency in radio tagging and radio tracking *Mustela* before reintroductions of black-footed ferrets. Studies of captive Siberian polecats and of reproductively sterilized polecats released into prairie dog colonies in Colorado and Wyoming provided opportunities to develop and test equipment. Radio collars made of natural materials were first tested on 13 captive polecats at the National Zoo's Conservation & Research Center, Front Royal, Va., during September 1989. Neckbands were made of leather or wool instead of the vinyl-coated fabric used previously. Collar retention was the primary reason for preliminary testing of radio collars on captive ferrets. Wool and leather collars are somewhat elastic, and the >10 percent stretch of these materials might allow animals to slip out of the collars. Overlapping ends of wool and leather collars were glued with contact cement. The transmitter package for polecats weighed about 10 g, had a 15.2-cm whip antenna (table 1, version D-2), and was attached to a 1-cm-wide wool collar with vinyl tape (not Teflon). The 2-stage, 3-V transmitter had a mercury switch that triggered change in pulse rate, resulting in pulse intervals of about 0.9–2.4 seconds, with pulse interval inversely proportional to activity of the animal (as sensed by motion of the transmitter), and a pulse width inversely proportional to pulse interval to maintain consistent and predictable current drain. Battery longevity was about 59 days.

Both wool and leather collars were removed by some captive animals, but in most cases the shed collars were in poor condition. Captive polecats were housed in family groups and tended to chew and pull on each other's collars causing rapid wear that we did not expect to occur under field

Figure 8. A 13-g transmitter package (version D-1 of table 1) from Wildlife Materials, Inc. (Murphysboro, Ill.), with Teflon tubing covering most of the acrylic potting material (used on black-footed ferrets [*Mustela nigripes*] during 1984). Photograph by D. Biggins.

conditions. Wool collars were no more likely to be pulled off than were leather collars, but wool collars wore more quickly. Because the "breakaway" feature of wool was desirable, the wool collar was selected for testing on the released animals to evaluate retention and irritation. Under field conditions, only 1 of the 13 polecats removed its collar, but that animal did so twice. Whip antennas broke on collars worn by two polecats. One antenna became completely severed after 10 days on the animal, and a radio recovered from a dead polecat had several broken strands in its antenna wire. Our simple solution was to use slightly heavier wire and an extra layer of heat-shrink coating extending 1 cm above the point where the antenna protruded from the radio capsule. No sign of worn hair or neck abrasion was noted on recovered polecats; however, there were only a few days of wet weather during our polecat release study, and the soil was sandier than soil at the Meeteetse black-footed ferret study area. Therefore, the potential for mud accumulation on radio collars was not fully assessed. During a short wet period, a small amount of mud was found on the collar of one recaptured polecat, but the mud fell away easily. Poor survival of polecats hampered the evaluation of radio-collar performance in that study (Biggins, 2000a).

Additional polecats released in 1990 (*n* = 44) accumulated about 600 animal days wearing the type of radio collars described above (but with the modified antennas), combining the time that animals carried radio collars during arena conditioning with monitoring time after release. The wool collars continued to function well overall. One collar deteriorated rapidly and was lost from a polecat after only 2 weeks, perhaps because that animal (no. 34, wild caught in China) was exceptionally active. Several other animals lost collars, likely in part because of rapid weight loss after release, particularly with obese animals (Biggins, 2000a). One instance of neck abrasion was noted, and again it was with animal no. 34. That animal was recollared after losing her first transmitter collar; perhaps the tendency was to fit the second collar too tightly because of the prior loss.

The polecat from China (no. 34), radio tracked until the study ended, lost 50 percent of her body mass and her radio collar during the first several weeks postrelease. Perhaps that scenario helps explain the high rate of lost radio contact with wild-caught polecats (3/5 versus 5/39 for captive-bred polecats). Other factors also can cause loss of radio contact. Two recovered radio collars were damaged, presumably by the teeth of coyotes (*Canis latrans*). The signal from one of those collars was barely audible above ground, even at short range (<100 m), suggesting the possibility of complete radio failure from bites of coyotes or badgers (*Taxidea taxus*). Radio signals also can be lost when animals are in burrows >2 m below ground. Because loss of radio contact could have been a result of predation, dispersal, or premature transmitter failures, functional longevity for collars could not be estimated.

Similar versions of these transmitters with wool collars also were used to study free-ranging Siberian polecats (fig. 9) (Zhou and others, 1994) and alpine weasels (*Mustela altaica*) in China (fig. 10). Collars of wool functioned well generally, but premature collar loss and occasional neck abrasions continued to be problems. Collar loss was especially common in the alpine weasel study (Wei and others, 1996). The polecat transmitter packages with variable pulse rates used in China and the United States produced easily interpreted activity data.

Figure 9. Additional collar tests (version D-2 of table 1) were conducted on a subspecies of free-ranging Siberian polecat (*Mustela eversmannii dauricus*) in Inner Mongolia, China. Photograph by D. Biggins.

Figure 10. We used smaller transmitters with wool collars to study alpine weasels (*Mustela altaica*) in Qinghai, China. Photograph by D. Biggins.

Because of the effective combination of wool collars and activity-type transmitters used on polecats, this 10-g unit by Wildlife Materials, Inc., (WMI, Murphysboro, Ill.) and a similar variable-pulse rate model by AVM Instrument Company, Ltd., (Colfax, Calif.) (table 1, version A-2) were adopted for monitoring 37 of 49 black-footed ferrets released during the first reintroductions in 1991 at Shirley Basin, Wyo. (U.S. Fish and Wildlife Service, 1992). Collars were worn by ferrets for 2–4 weeks before they were released, allowing prerelease observation of animals but also expending 40–68 percent of the expected battery life and producing noticeable wear to the wool collars.

Fluctuations in mass of animals appeared to create problems. Ferrets from the Henry Doorly Zoo (Omaha, Nebr.) were 26 percent heavier when collared than were their wild counterparts at Meeteetse ($P < 0.001$) and were 37 percent heavier at 5 days postcollaring. Seven of the zoo ferrets developed neck sores while being held in cages, perhaps because of the increasingly snug fit of the collars as the ferrets gained mass. Ferrets raised at the Wyoming Game and Fish Department facility were not heavier than Meeteetse ferrets prerelease. We accumulated 460 animal days of postrelease telemetric monitoring on the 37 ferrets. Loss of mass postrelease (Biggins, 2000a) likely loosened the fit of collars and may have exacerbated premature collar loss that occurred in nine known instances involving six individual ferrets (ferrets were sometimes recollared). One free-ranging ferret had a neck laceration when recaptured, but other injuries confused determination of the cause(s). There were two known cases of mud adhering to the vinyl tape used to attach the transmitter package to the collar.

Continued problems with collars in 1991 resulted in a more conservative approach to collar configurations used for ferret studies in subsequent years. Beginning in 1992, ferrets were collared with smaller transmitter packages, and Teflon heat-shrink tubing became the standard method for attaching the transmitter to the double- or triple-layered wool collar (fig. 11). The WMI transmitter had a 20.3-cm flexible steel whip antenna (table 1, version D-3). We located an improved type of stainless steel wire for whip antennas (designed for operating prosthetic limbs) that further reduced the problem of breakage resulting from metal fatigue. The 1.5-V battery gave an estimated 45–150 days of transmitting, depending on power output desired. The completed package weighed 6.0–7.2 g (usually <1 percent of the subject's mass). We believe that miniaturization of the transmitter-collar assembly reduced problems of collar loss and neck abrasion in black-footed ferrets. See appendix for instructions on final assembly of these collars and the procedure for fitting them to ferrets.

Figure 11. Fitting a lightweight (6–7 g) transmitter collar (version D-3 of table 1) to a black-footed ferret (*Mustela nigripes*). This style of collar has been used since 1991. Photograph by R. Reading.

Serious neck injuries may be caused by improper fit of radio collars; abrasions on radio-collared black-footed ferrets in 1991 fueled controversy over effects of collars on survival of ferrets. Oakleaf and others (1993), using data generated from spotlight searches after the second ferret release in 1992, stated that "survival indices are significantly ($P = 0.002$–0.055) greater for black-footed ferrets released without telemetry compared to ferrets released with telemetry collars." These authors presented four criteria that should be met to enhance comparability of collared and noncollared groups in future studies. Data for their analyses were generated under conditions that violated two of their criteria, similarity in habitat quality and equal accessibility for spotlight searches in areas where radio-collared and noncollared ferrets are released. Radio-collared ferrets were released on lower quality habitat, as measured by densities of prairie dog burrows, than were noncollared ferrets, and the areas with collared ferrets were less easily searched via spotlighting. Prior recognition of the possibility of confounding can be inferred from the hypothesis generated before the 1992 release of ferrets, which stated that "survival of ferrets released in best habitat, without telemetry and with good logistics for spotlight surveys is higher than survival in habitat that is possibly less than the best, with telemetry, and possibly poorer conditions for spotlighting" (B. Oakleaf, quoted in Miller and others, 1996, p. 129). Regarding habitat quality, mounting evidence demonstrates a negative correlation between ferret dispersal and density of prairie dog burrows (Biggins and others, 1999; Biggins, 2000b), and ferrets prefer areas with high burrow density (Biggins, Godbey, Matchett, and Livieri, this volume).

Confounding of collar effect and other variables was problematic in the 1992 sample involving 89 ferrets but became less troublesome as sample size increased because the potentially confounding variables were not consistently associated with the same primary treatment groups. Thus, it may be revealing to examine a much larger data set of reencounters, resulting from spotlight surveys about 1 month postrelease, for 724 ferrets released in four States during 12 years (table 2). For all States except Wyoming, cage-reared ferrets were excluded from the analysis because ferrets that lack preconditioning in outdoor pens have relatively poor survival rates (Biggins and others, 1998a). We could not categorize rearing status for some of the ferrets released in Wyoming; thus, we pooled rearing categories in Wyoming (similar to the analysis of Oakleaf and others, 1993). A multivariate general model (with site-year and mark category) and competing nested submodels were evaluated with program SURVIV (White, 1983). Comparisons of Akaike's Information Criteria (AIC) associated with these models (table 3) favored either the submodel that pooled collared and noncollared ferrets (AIC = 52.86) or the general model (AIC = 51.14). Not surprisingly, reencounter rates (the product of probabilities of survival and capture) for sites-years were likely different. Although

Table 2. Numbers of black-footed ferret (*Mustela nigripes*) kits released with and without radio collars. Assessment included only preconditioned kits (except in Wyoming).

	Montana		South Dakota		Utah		Wyoming		
Year	**No radio**	**Radio**	**No radio**	**Radio**	**No radio**	**Radio**	**No radio**	**Radio**	**Total**
1991							12	37	49
1992							52	37	89
1993							48		48
1994		17	7	6			37		67
1995		35		37					72
1996	28			39					67
1997			2	57					59
1998			41	42					83
1999				30	35	18			83
2000					27	29			56
2001					35	8			43
2002					8				8
Total	28	52	50	211	105	55	149	74	724

Table 3. Modeling minimum short-term (1 month) survival rates of 392 radio-collared and 332 noncollared black-footed ferrets (*Mustela nigripes*) released in Montana, South Dakota, Utah, and Wyoming.

Model	Log-likelihood	np[a]	AIC[b]
General	-17.534357	8	51.06871
All same	-92.542614	1	187.08523
Collaring same	-22.228649	4	52.45729
Sites-years same	-85.786658	2	175.57332

[a] np = number of parameters.

[b] AIC = Akaike's Information Criterion.

evidence was somewhat equivocal regarding collars, the most parsimonious model of the two with low AIC values suggested no effect of collars (fig. 12). Regardless of improvements in sample size and reduced confounding potential, this remains a post hoc analysis of data from experiments designed to test other hypotheses. Interactions are probable (fig. 12) and the unbalanced design (table 2) allows numerous possible explanations to account for the disparate results for different sites and years. Nevertheless, these data do not support the contention that radio collars negatively affect reencounter rates of released black-footed ferrets. Perhaps cases of management intervention enabled by radio telemetry help compensate for potentially negative influences of collars. On a few occasions, ferrets that dispersed from suitable habitat were captured and translocated; other interventions (also rare) included capture, rehabilitation, and rerelease of ferrets that were injured or in poor condition.

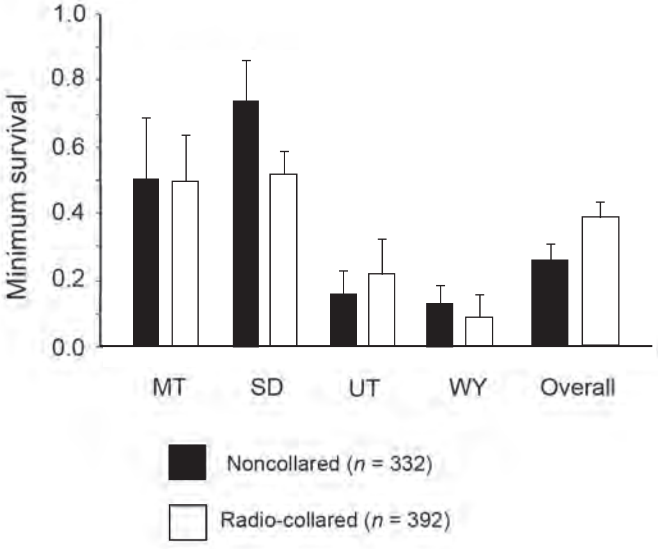

Figure 12. Minimum survival rates of preconditioned black-footed ferret (*Mustela nigripes*) kits at about 1 month postrelease.

In a study of translocated ferrets conducted in South Dakota in 1999 (Biggins and others, 2000a), neck abrasions that ranged from minor hair loss to a case of severe ulceration were noted on 10 radio-tagged black-footed ferrets (of 36 released) when animals were reobserved during the study or recaptured for collar removal at the end of the study. A categorical variable (abrasion, no abrasion) for neck condition was evaluated during statistical modeling to assess movements and dispersal of the primary treatment groups (released captive-reared versus wild-born ferrets). There was no evidence that neck abrasions affected any of the attributes of movements examined ($P > 0.19$ for all models), even though the experimental design and statistical analyses were sufficiently powerful to detect significant effects of several other variables.

In summary, collar-caused mortality of ferrets has not been documented, and there is no evidence of negative effects of radio telemetry on ferret populations or average behaviors within groups of ferrets. Nevertheless, collaring can at times negatively impact individual ferrets. Moreover, it seems best to assume, even without the latter evidence, that an unnatural protuberance of any sort will influence a free-ranging animal's behavior to some degree, even if that influence is not detectable statistically. Such influences may be acceptable, particularly if it can be reasonably assumed that they equally affect all treatment groups of an experiment. Decisions on whether or not to use this monitoring tool may rest with cost/benefit analyses. If information potentially gained could enhance success of future conservation of the ferret, risk to individuals may be warranted. The arguments, however, appear similar to those discussed with reference to releasing adult ferrets (Biggins, Godbey, Livieri, and others, this volume), wherein "some conservationists and ethicists may justify extreme means to achieve the goal of preservation and recovery" of a species, while "others may set inviolate moral standards regarding the welfare of individuals."

Compared to other recent studies of *Mustela* that have involved radio telemetry, our present collars have rather conservative dimensions and mass. Considering *Mustela* of sizes similar to black-footed ferrets, 27-g and 25-g collars were fitted to feral domestic ferrets in New Zealand (Moller and Alterio, 1999; Byrom, 2002), collars of 25–35 g were placed on European polecats (*M. putorius*) in Italy (Marcelli and others, 2003), and endangered European mink (*M. lutreola*) were tagged with collars of about 13 g in Spain (Zabala and others, 2003). Collars weighing 10 g (likely 4–6 percent of body mass) were placed on stoats (*M. erminea*) in New Zealand (Moller and Alterio, 1999). Although Jedrzejewski and others (2000) tagged least weasels (*M. nivalis*) in Poland with collars of only 3.5–4.5 g, that mass was about 4 percent of the body mass of their subjects. Realizing the sensitivity of these animals to handling and collaring, the latter investigators placed the weasels into an enclosure for several days of observation before final release at the location of capture. We are aware of problems of collar loss and neck abrasion caused by radio collars in other studies of radio-tagged *Mustela*, although discussions of such difficulties are seldom published.

Problems with collars precipitated evaluations of intraperitoneal and subcutaneous implants for black-footed ferrets. Surgically implanted transmitters have been used effectively in several other mustelids such as river otters (*Lutra canadensis*; Hoover, 1984), badgers (Minta, 1993; Goodrich and Buskirk, 1998), and American mink (*Mustela vison*; Stevens and others, 1997). In 1985, we solicited prototype implantable transmitters suitable for ferrets from radio-telemetry equipment suppliers. Two of these units were designed for intraperitoneal use (table 1, versions D-5 and E-2), and a smaller unit (table 1, version D-4) was to be used subcutaneously. All had disappointingly low power output, leading us to believe that the problems we had in 1991 with loss of contact with ferrets would be worse with the implanted transmitters. Power output of the implants was initially lower than even that of the first radio collars used (table 1) and could be expected to be further degraded after implanting by signal attenuation caused by the ferret's body. Thus, we did not proceed to the next planned step in tests, which was to surgically implant the transmitters into surrogate Siberian polecats.

We did, however, use intraperitoneal and subcutaneous implants in American badgers at the Meeteetse study area in 1984. The dorsally implanted subcutaneous units with 15.2-cm implanted whip antennas radiated more powerful signals than did intraperitoneal units in the same animals, but abscesses that developed around the subcutaneous transmitters resulted in their premature loss. Compared to signals from the radio-tagged ferrets, which were then carrying relatively powerful transmitters (table 1, version D-1), signals from the subcutaneous implants in badgers were about as easily received from our fixed stations, but the intraperitoneal implants in badgers were much more difficult to track. Allowing that technology might have improved during the subsequent decade, we repeated the process of acquiring prototype implantable transmitters for ferrets in 1997, with generally similar results. Relatively poor reception range is a well-known attribute of implantable transmitters, in part because of the compromises necessary with transmitter antennas, which can translate into reduced precision and accuracy of data (Koehler and others, 2001). In our case, low power output resulted in rejection of implant technology before it was necessary to weigh the additional risks and costs of the surgeries needed for implanting and removing the transmitter. It also would have been necessary to consider the possible impact of implants on fertility of females and the possibility that implanted ferrets might not be locatable when it was time to remove the transmitter.

Radio-tracking Strategies

We quickly realized after radio tagging the first black-footed ferret in 1981 that signal-following techniques using hand-held tracking equipment were unlikely to generate the type, quality, and volume of data we were seeking. Much time was wasted searching for the subjects given the combination of relatively inefficient receiving antennas and low power output from the transmitters. Aside from the partial solution of developing more powerful transmitters (discussed above), it also was necessary to use much more directional and sensitive receiving antennas in order to maintain contact with the ferrets. Also, our signal-following attempts at night often appeared to disturb the ferrets. Thus, we decided to develop several stations of varying mobility equipped with larger antenna arrays from which tracking could be remotely accomplished via triangulation. Camper trailers with dual-beam 11- or 12-element, rotatable Yagi antennas (fig. 13) became the mainstay of the tracking system, augmented by more mobile truck-mounted receiving equipment (fig. 14). The relatively high receiving efficiency of these stations resulting from the larger antennas was further enhanced by increasing the heights of the arrays with masts of 4.5–6.0 m and by placing the stations on hilltops whenever possible. Although reception range was highly variable for these stations and the transmitters that were developed later (table 1, version D-3), we commonly radio-tracked ferrets at distances of 0.5–2.0 km and received signals from as far as 26.0 km on occasion (Biggins and others, 1999).

Knowing the exact locations of stations is a prerequisite for accurate triangulation. These data were produced (in Universal Transverse Mercator coordinates) by using traditional survey techniques (transit and chain) in the 1980s, followed by location data from a differentially corrected Global Positioning System in later years. Meticulous accuracy testing of each station improved the data in two ways. First, such tests allowed assessment of bias patterns inherent in each station and development of correcting algorithms to improve accuracy of data during processing. Second, the residual variation in bearings from stations, after bias was corrected, allowed estimates of accuracy to be associated with each estimated location for a ferret. Tests were conducted by contrasting telemetric bearings to 60–100 beacon transmitter locations surrounding the tested station with a set of known bearings to those beacon locations measured with a surveyor's transit (fig. 15). We employed a split sample technique to analyze test data, using half of the sample to derive the bias corrections and the second half to assess residual variation after the corrections were applied (fig. 16).

Figure 13. Camper trailer fitted with rotatable, 11-element, dual-beam Yagi array, used to radio track black-footed ferrets (*Mustela nigripes*) at the Meeteetse, Wyo., study area in 1983–84. Photograph by D. Biggins.

Figure 14. Truck-mounted, collapsible, 5-element Yagi array used to radio track black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyo., during 1982–84. Photograph by D. Biggins.

A second prerequisite for accurate triangulation is the ability to reference bearings from the antenna. Bearings can be usefully processed only when they are relative to a known

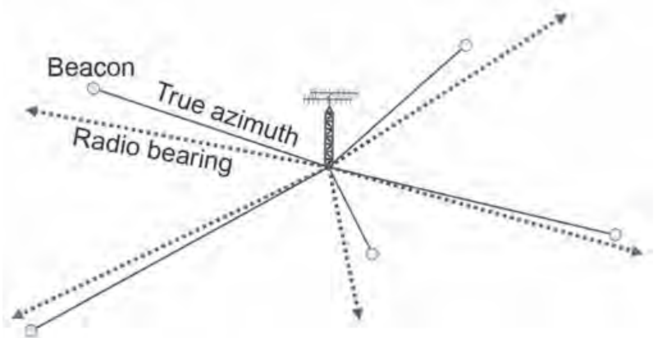

Figure 15. Accuracy testing and referencing involve comparison of true azimuths and radio bearings to beacon transmitters.

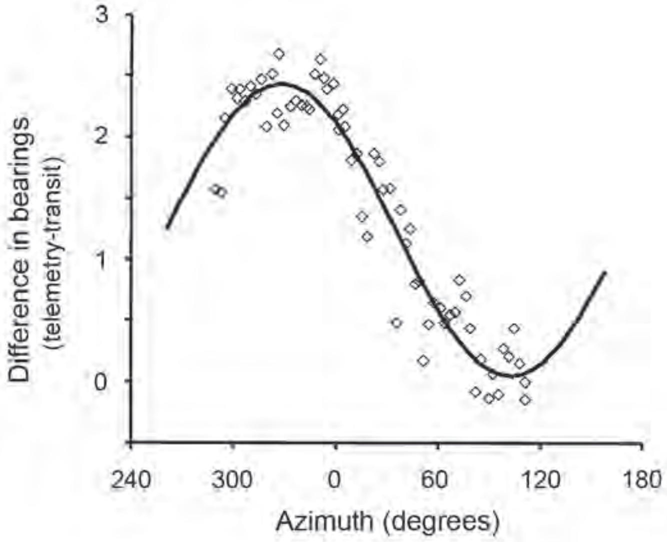

Figure 16. An accuracy test done at station 4, UL Bend National Wildlife Refuge, Mont., 1994. In this case, bias was corrected by using a formula defining the sine curve plotted. Residual variation produced a bias-adjusted accuracy estimate of ±0.63º (90% confidence) for future bearings from this station.

entity, such as grid north. One could simply align the main beam of the antenna to north with a compass and set the compass rose to zero. This method is rather crude (White and Garrott, 1990); at least two problems cause variable results. First, the physical and electronic alignment of antennas is seldom absolutely parallel. Second, there is considerable variation in the electronic aiming (fig. 16). If one could successfully get the aim exactly right at one particular point on the compass rose, then it would still not be correct for many other points around the compass rose. Some sort of averaging is needed. To solve these problems, we used reference transmitters placed at known points in the study area. Actual azimuths to the beacons were known for each station and were compared to the telemetric bearings to those transmitters (fig. 15), taken at the beginning of each tracking session. The compass rose inside a station was set so that zero was approximately at grid north (e.g., using a compass), and then readings to multiple beacons were used to provide an average correction that was applied to each subsequent bearing on an animal. Bias adjustment was applied before the referencing correction was made, the same as the process used when animals were tracked. Because the accuracy of this procedure affects all subsequent data, we cannot overemphasize the care needed in referencing. It would be nice to have many beacon transmitters (e.g., 50)! In practice, we used three to six beacons to avoid allowing referencing to become the dominant feature of a tracking session.

Although it is possible to plot triangulation data from pairs of these stations directly on maps to ascertain the whereabouts of the ferrets being tracked, it is more accurate and faster to process these data via computer. Advantages of conducting at least some of this processing while radio tracking include the following: (1) station selection can be adjusted as animals being tracked move about; (2) radio-tracking errors can be detected in time to correct them; (3) instances of mortality can be recognized quickly, resulting in better diagnoses of causes; (4) ferret dispersal can be detected in time to allow remedial action, if desired; and (5) in the case of lost radio contact, the last location calculated gives a starting point for searches. A computer program written by one of us (DEB) to accomplish these field processing tasks assisted the technicians with radio tracking ferrets at Meeteetse. The program was used on a programmable calculator in 1982 and was adapted to the first laptop computers that became widely available in 1983. That program evolved into TRITEL (Biggins and others, 2000b), which has been repeatedly modified since 1983 to accomplish referencing and bias corrections, convert azimuth data into coordinates, calculate error estimates for each telemetric fix (fig. 17), and store resulting data.

Procedures for radio tracking and processing data are detailed in a separate report (Biggins and others, 2000b). We have relied on intensive triangulation from these kinds of stations to produce large volumes of data. Although we have at times recollared ferrets to extend data gathering over several months, all telemetric studies were relatively short term. To monitor reintroductions, ferrets often were radio tracked for just 2–4 weeks postrelease, but stations were usually occupied during all hours of the day or during all hours of darkness, with fixes generated by occupants at two or more stations coordinating their tracking with two-way radio communication. Intensity of re-location for individual ferrets varied (3–60 minutes between consecutive fixes on an individual), depending mostly on how many individual animals were being monitored. During the reintroduction phase of black-footed ferret recovery (1989–2000), we used this tracking strategy

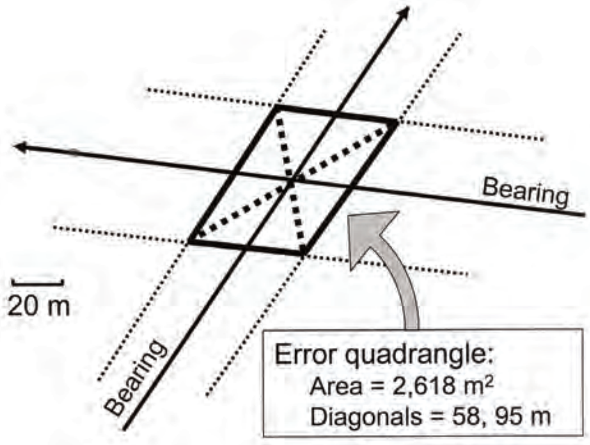

Figure 17. An example of a telemetric fix and error quadrangle (black-footed ferret [*Mustela nigripes*] no. 26, South Dakota, 10/23/97, 0148 h) produced by intersecting bearings and their associated error arcs from two tracking stations.

to monitor 340 radio-tagged ferrets and polecats, accumulating 83,275 lines of data that included 44,191 indications of status and 39,084 estimates of location (fixes). Data on status demarked beginning and ending points of tracking sessions, activity of animal (active, inactive) as determined by variation in signal strength, and pulse interval records when transmitters with variable pulse rates were used. Status data were recorded with fixes but were the only data recorded when triangulation was not possible (e.g., when only a single station received an adequate signal).

Radio-telemetry data from triangulation allows many options for analyses (summarized by White and Garrott, 1990). For black-footed ferrets, we have used radio telemetry to examine survival rates (Biggins, 2000a), linear movements (Biggins and others, 1999), dispersal (Biggins, Godbey, Livieri, and others, this volume), habitat preferences (Biggins and others, 1985; Biggins, Godbey, Matchett, and Livieri, this volume), indices of spatial use (Biggins and others, 1998b), and activity cycles (Biggins and others, 1986; Biggins, 2000a). The examples noted above are not exhaustive, and other options for use of the large data sets generated during multiple studies are currently being pursued. We believe that several features of analyzing telemetric data for ferrets, however, are worthy of emphasis here.

First, the inevitable errors that occur during triangulation must be detected and eliminated to the extent possible. Our system for handling data from triangulation, consistent with a pattern noted by Kenward (1987), has resulted in a series of custom computer programs for manipulating the output from TRITEL and screening for errors (Breck and Biggins, 1997). Similar to the BIOCHECK routine of White and Garrott (1990), our error screening involves searches for nonsensical data entries (e.g., unreasonable dates or times) and for data that fall outside limits set by a priori knowledge of ferret behaviors (e.g., maximum speed of movement). Errors are either corrected by referral to original data sheets, or offending lines are removed.

Second, estimates of ferret locations derived from triangulation are subject to direction-finding variation, as noted above. Estimates of such error associated with each fix (“error quadrangles” when two stations are used) are stored with each fix when TRITEL is used to process bearings. Our error screening process removes data lines with error estimates exceeding specified limits for lengths of diagonals or area of the quadrangle. Just as importantly, we have used these attributes of error as covariates in multivariate statistical analyses and often retain them in statistical models as “control” variables even if their estimated effect is small or not statistically significant. Although tracking error is nuisance variation when one is attempting to assess other treatments, it often accounts for significant variation (Biggins and others, 1998b, 2000a; Biggins, 2000a). If, however, a response variable is already known to be positively correlated to tracking error, then the use of tracking error as a covariate is not warranted. An example is dispersal. Because error is in part a function of distance separating station and subject, sizes of the error quadrangles increase as ferrets disperse away from tracking stations. Unlike other movements within the monitored area, radio-tracking error should not be used to explain variation in dispersal by ferrets because increased tracking error is an expected consequence of dispersal.

Third, the ferret data we have generated are serially correlated because of short interfix intervals; each telemetric fix cannot be considered independent (Swihart and Slade, 1985). The level of detail present in our data sets allows powerful behavioral comparisons (see examples cited above), but caution must be exercised in analyzing these data when independent observations are required (e.g., home range estimation; see White and Garrott, 1990).

The close association between black-footed ferrets and prairie dog colonies facilitates the radio tracking of ferrets from fixed tracking stations. Ferrets often remain within predictable boundaries where radio tracking coverage was nearly complete with careful placement of multiple stations (e.g., the Montana study of Biggins, Godbey, Matchett, and Livieri, this volume). Nevertheless, if we would like to monitor every animal in our sample with equal intensity and accuracy, triangulation from fixed stations is problematic (not unlike data from any other method of radio tracking or monitoring). Signal quality and accuracy of fixes vary with range and topography, and positioning of stations interacts with these factors to create uneven trackability of animals throughout any study area. The movements of some animals may be described more accurately and completely than the movements of others, and probabilities of detecting mortality cases may vary accordingly. Animals that disperse away from fixed stations may be tracked with lower intensity, lower accuracy, or not at all. Attributes such as cumulative movements are affected by frequency and accuracy of relocations. The consequences can be serious if the goal is to characterize the behaviors of the species. When comparing treatment groups (e.g., sexes, ages, rearing treatments), the consequences are more benign if we can reasonably assume that animals are distributed in the study area in such a way that members of each group are about equally trackable on average. The possibility of group-specific biases should be carefully considered for each case. For example, if dispersal is the attribute of interest, it may or may not be logical to rely on data from fixed-station triangulation. If dispersal distances have been artificially truncated by reception range of the tracking system, power of a comparative experiment may be reduced and dispersal distances will be underestimated to the greatest degree for groups whose members tend to disperse most frequently and farthest. Nevertheless, radio tracking from fixed stations has enabled us to detect significant between-group differences in dispersal (Biggins and others, 1998b, 1999). A germane statistical adage might be “if the tree falls, the axe was sharp enough” (Martin and Bateson, 1990, p. 126).

We have augmented triangulation with hand tracking, automated signal monitoring and data logging, and tracking from aircraft. Hand tracking, usually with a hand-held receiver and a 3-element Yagi antenna, was often used to investigate ferrets whose transmitters (a) were in unusual locations, (b) had moved rapidly, (c) had not been detected for long periods, (d) were stationary above ground at night, or (e) were above ground during daytime. These circumstances often led to re-location of ferrets that had dispersed (fig. 18) or to ferrets that had been killed by predators (fig. 19; Biggins, Godbey, Livieri, and others, this volume). We attempted to visit the location of the last fix if contact with a transmitter was lost for 2 or more days; listening for a radio signal while walking a narrowly spaced grid (ca. 2-m spacing) sometimes allowed detection of the transmitter belowground to depths of >4 m. Signal strength was correlated with depth of the transmitter; weakest signals could be received only when the operator was almost directly above the transmitter with the Yagi antenna pointing vertically downward (Biggins, 2000a). Signals seldom emanated from burrow entrances (contrary to the predictions of some electronic engineers). Remains of badger-killed ferrets were located by careful searches and excavated (fig. 20). Lost contact with transmitters also precipitated aerial searches at some sites. Each aircraft was equipped with a pair of 4-element Yagi antennas (affixed to each wing strut) and a switch to allow the operator to listen to the signal from each antenna separately. Homing on the source of a signal was accomplished by equalizing the null from each antenna (Gilmer and others, 1981). Radio-tracking flights helped locate ferrets that dispersed to different prairie dog colonies, especially when the flights were at night when ferrets are

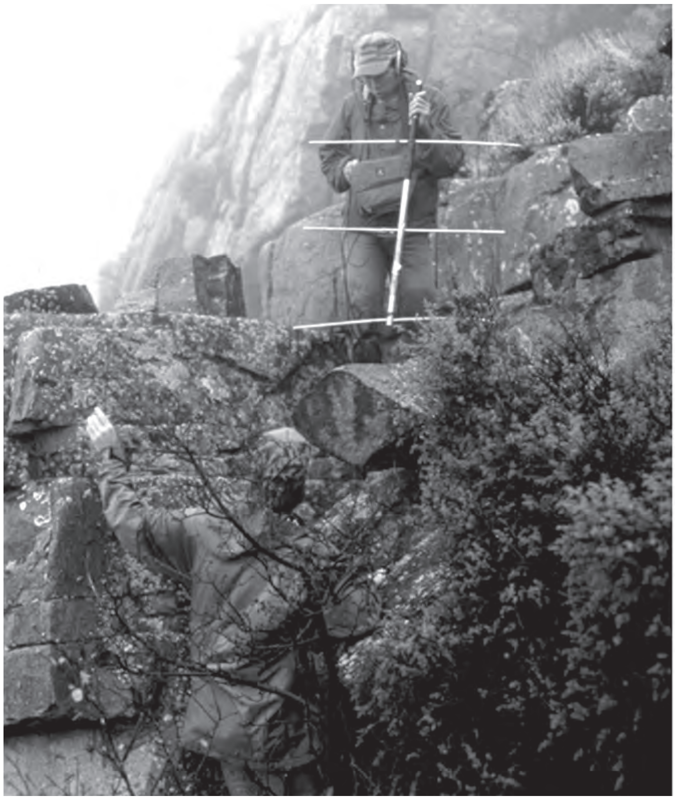

Figure 18. Hand tracking enabled us to locate black-footed ferrets (*Mustela nigripes*) that had dispersed into unusual habitats. Photograph by M. Albee.

Figure 19. Siberian polecat (*Mustela eversmannii*) killed by a predator. Photograph by D. Biggins.

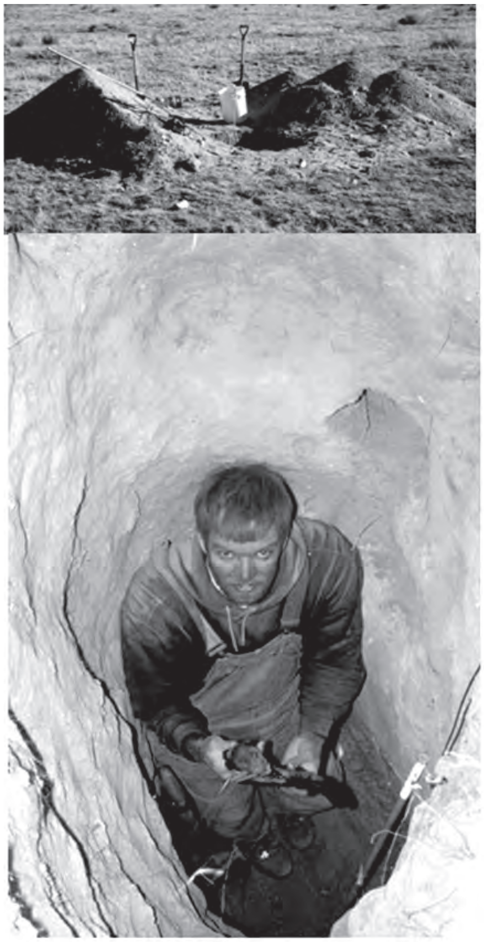

Figure 20. Hand-held tracking equipment enabled location of transmitters below ground, necessitating excavation to determine fate of animals such as this Siberian polecat (*Mustela eversmannii*) killed by a badger (*Taxidea taxus*). Photographs by D. Biggins.

most active above ground (Biggins and others, 1986; Biggins, 2000a). The most common product of flights, however, was detection of lost collars and cases of aboveground predation on ferrets that had dispersed (or their transmitters had been dispersed by the predator) beyond signal reception range of tracking stations. In short, these follow-up techniques, although arguably less technologically demanding than the radio tracking by triangulation, have provided the critically important details on fates of animals that other strategies cannot produce.

We used signal monitoring both with automated chart recorders and with computer loggers in attempts to collect information on aboveground activity of ferrets and polecats (Biggins, 2000a). The technique was useful to supplement data from triangulation, particularly on animals that were beyond the boundaries of the area that could be effectively monitored by tracking stations; however, the relative insensitivity of automated systems to detection of weak signals, coupled with the large activity areas of black-footed ferrets, limits the utility of automated tracking for ferrets.

Summary

The wide range of problems and accomplishments accompanying the use of radio telemetry on ferrets provides an opportunity for both detractors and proponents to present powerful arguments. Although success was never close to total, failures were not devastating to data or the ferrets. We would like to reemphasize that radio telemetry is an expensive and labor-intensive method for monitoring black-footed ferrets and that attaching radio transmitters to ferrets poses risks to the animals. It is essential, therefore, to carefully consider the objectives of a study to ascertain whether other tools would suffice. Justifications for use of radio telemetry on ferrets include unexplained lack of success in establishing a ferret population and tests of hypotheses that have large-scale management implications and require behavioral information. Cost/benefit analyses regarding use of telemetry should include as costs the potential future losses of ferrets if a perceived need for information remains unfulfilled. In some cases, short-term recovery objectives may become subordinate to learning objectives that could advance long-term recovery goals.

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References Cited

Biggins, D.E., 2000a, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., 2000b, Dispersal of radio-tagged black-footed ferrets released on prairie dog colonies in Wyoming, Montana, and South Dakota [abs.], *in* Proceedings of the 2000 Annual Meeting: Vernal, Utah Chapter of the Wildlife Society.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998a, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Godbey, J.L., Horton, B., and Livieri, T.M., 2000a, Experimental translocation of wild-born black-footed ferrets in South Dakota: Fort Collins, Colo., Fort Collins Science Center, U.S. Geological Survey, 14 p.

Biggins, D.E., Godbey, J.L., and Matchett, M.R., 1998b, Behavior and survival of black-footed ferrets (*Mustela nigripes*) when captive-born young were released into a free-ranging population: Fort Collins, Colo., Fort Collins Science Center, U.S. Geological Survey, 25 p.

Biggins, D.E., Hanebury, L.R., Godbey, J.L., and Miller, B.J., 2000b, Radio-triangulation and program TRITEL for wildlife research—an instruction manual: Fort Collins, Colo., Fort Collins Science Center, U.S. Geological Survey, 57 p.

Biggins, D.E., Schroeder, M., Forrest, S., and Richardson, L., 1985, Movements and habitat relationships of radio-tagged black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 11.1–11.17.

Biggins, D.E., Schroeder, M.H., Forrest, S.C., and Richardson, L., 1986, Activity of radio-tagged black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 135–140.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Breck, S.W., and Biggins, D.E., 1997, Detecting and eliminating errors in radio-telemetry data sets—a comparison of screened and unscreened data [abs.], *in* Forum on wildlife telemetry—innovations, evaluations, and research needs: Jamestown, N. Dak., Northern Prairie Wildlife Research Center, U.S. Geological Survey, p. 15.

Byrom, A.E., 2002, Dispersal and survival of juvenile feral ferrets *Mustela furo* in New Zealand: Journal of Applied Ecology, v. 39, p. 67–78.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Erickson, R.C., 1973, Some black-footed ferret research needs, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 153–164.

Erlinge, S., 1979, Movements and daily activity pattern of radio tracked male stoats (*Mustela erminea*), *in* Amlaner, C.J., and Macdonald, D.W., eds., A handbook on biotelemetry and radio tracking: Oxford, U.K., Pergamon Press, p. 703–710.

Fagerstone, K.A., and Biggins, D.E., 1986, Summary of black-footed ferret and prairie dog research conducted by the Denver Wildlife Research Center, 1981–1985: Denver, Colo., Denver Wildlife Research Center, U.S. Fish and Wildlife Service, 31 p.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Gaynor, J.S., Wimsatt, J., Mallinckrodt, C., and Biggins, D., 1997, A comparison of sevoflurane and isoflurane for short-term anesthesia in polecats: Journal of Zoo and Wildlife Medicine, v. 28, p. 274–279.

Gilmer, D.S., Cowardin, L.M., Duval, R.L., Mechlin, L.M., Shaiffer, C.W., and Kuchle, F.B., 1981, Procedures for the use of aircraft in wildlife telemetry studies: U.S. Department of the Interior, Fish and Wildlife Service Resource Publication 140, 19 p.

Goodrich, J.M., and Buskirk, S.W., 1998, Spacing and ecology of North American badgers (*Taxidea taxus*) in a prairie-dog (*Cynomys leucurus*) complex: Journal of Mammalogy, v. 79, p. 171–179.

Hoover, J.P., 1984, Surgical implantation of radiotelemetry devices in American river otters: Journal of the American Veterinary Medical Association, v. 185, p. 1317–1320.

Jedrzejewski, W., Jedrzejewska, B., Zub, K., and Nowakowski, W.K., 2000, Activity patterns of radio-tracked weasels *Mustela nivalis* in Bialowieza National Park (Poland): Annales Zoologici Fennci, v. 37, p. 161–168.

Kenward, R.E., 1987, Wildlife radio tagging: San Diego, Calif., Academic Press, 222 p.

Kimmich, H.P., 1979, Artifact free measurement of biological parameters—biotelemetry, a historical review and layout of modern developments, *in* Amlaner, C.J., and Macdonald, D.W., eds., A handbook on biotelemetry and radio tracking: Oxford, U.K., Pergamon Press, p. 3–20.

Koehler, G.M., Hall, P.B., Norton, M.H., and Pierce, D.J., 2001, Implant- versus collar-transmitter use on black bears: Wildlife Society Bulletin, v. 29 p. 600–605.

Linder, R.L., and Hillman, C.N., preparers, 1973, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, 208 p.

Marcelli, M., Fusillo, R., and Boitani, L., 2003, Sexual segregation in the activity patterns of European polecats (*Mustela putorius*): Journal of the Zoological Society of London, v. 261, p. 249–255.

Martin, P., and Bateson, P., 1990, Measuring behaviour, an introductory guide: Cambridge, U.K., Cambridge University Press, 200 p.

Miller, B., Reading, R.P., and Forrest, S., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Minta, S.C., 1993, Sexual differences in spatio-temporal interaction among badgers: Oecologia, v. 96, p. 402–409.

Moller, H., and Alterio, N., 1999, Home range and spatial organization of stoats (*Mustela erminea*), ferrets (*Mustela furo*) and feral house cats (*Felis catus*) on coastal grasslands, Otago Peninsula, New Zealand—implications for yellow-eyed penguin (*Megadyptes antipodes*) conservation: New Zealand Journal of Zoology, v. 26, p. 165–174.

Oakleaf, B., Luce, B., and Hnilicka, P., 1993, Survival and dispersal of captive raised black-footed ferrets reintroduced in Shirley Basin, Wyoming. A comparison between black-footed ferrets released with and without telemetry collars, *in* Oakleaf, B., Luce, B., Thorne, E.T., and Williams, B., eds., Black-footed ferret reintroduction in Shirley Basin, Wyoming, 1992, Annual Completion Report: Cheyenne, Wyoming Game and Fish Department, p. 188–219.

Stevens, R.T., Ashwood, T.L., and Sleeman, J.M., 1997, Fall–early winter home ranges, movements, and den use of male mink, *Mustela vison*, in eastern Tennessee: Canadian Field-Naturalist, v. 111, p. 312–314.

Swihart, R.K., and Slade, N.A., 1985, Testing for independence of observations in animal movements: Ecology, v. 66, p. 1176–1184.

Thorne, E.T., Schroeder, M.H., Forrest, S.C., Campbell, T.M., III, Richardson, L., Biggins, D., Hanebury, L.R., Belitsky, D., and Williams, E.S., 1985, Capture, immobilization, and care of black-footed ferrets for research, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 9.1–9.8.

Ubico, S.R., Maupin, G.O., Fagerstone, K.A., and McLean, R.G., 1988, A plague epizootic in the white-tailed prairie dogs (*Cynomys leucurus*) of Meeteetse, Wyoming: Journal of Wildlife Diseases, v. 24, p. 399–406.

U.S. Fish and Wildlife Service, 1992, Reintroduction of the black-footed ferret (*Mustela nigripes*): Fort Collins, Colo., National Ecology Research Center, 44 p.

Wei, W., Zhou, W., Fan, N., and Biggins, D., 1996, Activity rhythm and home range of the alpine weasel (*Mustela altaica*): Acta Theriologica Sinica, v. 16, p. 35–42.

White, G.C., 1983, Numerical estimation of survival rates from band-recovery and biotelemetry data: Journal of Wildlife Management, v. 47, p. 716–728.

White, G.C., and Garrott, R.A., 1990, Analysis of wildlife radio-tracking data: San Diego, Calif., Academic Press, 383 p.

Zabala, J., Zuberogoitia, I., Garin, I., and Aihartza, J., 2003, Landscape features in the habitat selection of European mink (*Mustela lutreola*) in south-western Europe: Journal of the Zoological Society of London, v. 260, p. 415–421.

Zhou, W., Wei, W., and Biggins, D.E., 1994, Activity rhythms of polecats (*Mustela eversmannii*) in the Qing-Zang Plateau: Acta Biologica Plateau Sinica, v. 12, p. 173–187.

Appendix. Notes on Radio Collaring Black-footed Ferrets

Collars that we are presently using are considerably more fragile than their predecessors and are intentionally designed to lack durability. Most black-footed ferrets (*Mustela nigripes*) shed the collars within 2 months (often much sooner). Use of more durable collars seems to increase the risk of neck sores. Presently, collars 1 cm wide are made of 100 percent wool, folded into three layers and sewn with 100 percent cotton thread. The edges are not bound, so the wool will fray rapidly. After sewing the wool into long strips of uncut collars, we prestretch the material. It is soaked in water and hung to dry with a 200-g weight clamped to the lower end. Collars are then cut to 15–18 cm lengths. To attach a collar to the transmitter unit, both are inserted into a 2.5-cm length of Teflon® heat-shrink tubing (1.25 cm diameter), and a heat gun (or other heat source such as a gas stove or propane torch) is used to shrink the tubing. Overheating the transmitter packages can cause malfunctions. High temperature for a short duration works better than less heat applied for longer times. The object is to heat the tubing without overheating the transmitter and battery. After shrinking the tubing, the package is cooled rapidly by wrapping it in a cool, wet sponge. Equipment and supplies needed to attach these collars to ferrets include scissors, a hemostat clamp, contact cement, a telemetry receiver, and a hair dryer. Mustelids characteristically have little neck constriction, making exact collar fit important. The attachment procedure for black-footed ferrets may be accomplished in the following steps:

1. Remove the magnet and check transmitter operation.
2. Restrain ferrets with a light dose of ketamine/diazepam (about 17–20 mg per kg of body weight) for this noninvasive procedure (Thorne and others, 1985). Recently, we have been using isoflurane gas anesthesia, which is more controllable (Biggins, Godbey, Matchett, and others, this volume). New innovations in gas anesthesia (e.g., sevoflurane; Gaynor and others, 1997) have additional advantages but require different vaporizers. The U.S. Fish and Wildlife Service requires ferret handlers to be trained in anesthesia and handling procedures.
3. As soon as the animal is tranquil enough to handle, make a trial fit of the collar and mark the length needed, allowing about 1-cm overlap of ends. Mark the area of overlap that will be glued, but do not trim excess from the long end of the collar until later. The extra length makes it easier to fit on the animal and can be trimmed at the end of the process.
4. Coat the inside of one end and the outside of the other end with contact cement. We use the Weldwood® (DAP® Products, Inc., Baltimore, Md.) version that has a toluene solvent, which seems to work better than the versions with other solvents. The glue-drying process takes 3–10 minutes. A hair dryer speeds drying. The first coat of cement normally penetrates the wool. Unless the glue is quite thick, the first coat must be dried completely and a second coat applied and dried until tacky.
5. Wrap the collar around the animal's neck and press a tiny portion of the glued strip together lightly. This process allows a final check for snugness before the final gluing is done. Collar fit is critical; it should be snug but not tight. The collar should rotate fairly easily around the neck. Also, a small closed hemostat or small scissors should slide easily between the neck and collar, but if you can insert your little finger, the collar is probably too loose.
6. If the fit seems satisfactory, press the glued ends together firmly. Use the hemostat to clamp the ends, repeatedly clamping and releasing until the entire overlap area has been pressed together firmly. Trim excess wool from the long end of the collar. We know of only one occasion when the glue joint failed, and that was when a technician did not realize that he had to let the glue dry before pressing the ends together. In fact, we have not been able to separate the final joint by pulling the ends apart—the material always tears. It may even be difficult to separate the ends during the trial fitting if they have made too much contact.

Postrelease Movements and Survival of Adult and Young Black-footed Ferrets

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Abstract

A successful captive breeding program for highly endangered black-footed ferrets (*Mustela nigripes*) has resulted in surplus animals that have been released at multiple sites since 1991. Because reproductive output of captive ferrets declines after several years, many adult ferrets must be removed from captive breeding facilities annually to keep total production high. Adults are routinely released, with young-of-the-year, on prairie dog (*Cynomys* spp.) colonies. We evaluated postrelease movements and survival rates for 94 radio-tagged young and adult ferrets. Radio-tagged adult ferrets made longer movements than young ferrets during the night of release and had significantly lower survival rates for the first 14 days. Coyotes (*Canis latrans*) caused the largest number of ferret losses. A larger data set of 623 ferrets represented adults and young that were individually marked with passive integrated transponders but were not radio tagged. Minimum survival rates, calculated primarily from ferrets detected during spotlight searches and identified with tag readers, again were significantly lower for adults than for young ferrets at 30 days postrelease (10.1 percent and 45.5 percent survival, respectively) and at 150 days postrelease (5.7 percent and 25.9 percent). Assessment of known survival time by using linear modeling demonstrated a significant interaction between age and sex, with greater disparity between adults and kits for females than for males. Postrelease survival of adult ferrets might be increased if animals were given earlier and longer exposure to the quasi-natural environments of preconditioning pens.

Keywords: age, behavior, mortality, *Mustela nigripes*, predation, radio telemetry

Introduction

Black-footed ferrets (*Mustela nigripes*) nearly became extinct when diseases invaded the last known free-ranging population near Meeteetse, Wyo., in 1985 (Lockhart and others, this volume). A rescue effort resulted in a captive population that has provided ferrets for reintroduction since 1991. The mean life expectancy of free-ranging black-footed ferrets in the ancestral Meeteetse population was about 0.9 years (calculated by using the negative reciprocal of the natural log of 0.34, an annual survival rate estimated by Forrest and others, 1988). With such a short average life expectancy, natural selection may have applied little pressure for sustained productivity in older age classes of ferrets. In captivity, productivity declines rapidly after ferrets are only a few years old (Williams and others, 1991). Efficient management of the captive breeding program thus involves relatively rapid rotation of animals (Marinari and Kreeger, this volume). Older animals are placed in zoos for exhibit and used for research, but the supply of such animals exceeds the demand. Adult ferrets are routinely released at reintroduction sites, a practice that has been criticized. Although both young and adult ferrets have been released at several sites, their postrelease movements and survival have not been compared. Marking of animals, spotlight searches, and identification of surviving ferrets are tools routinely used for monitoring at release sites (Biggins, Godbey, Matchett, and others, this volume), providing useful multiyear data sets. In certain years, more intensive radio-telemetry studies (Biggins, Godbey, Miller, and Hanebury, this volume) were directed at testing hypotheses regarding prerelease experience and rearing methods. Cumulative data from these former efforts provide the opportunity to contrast the movements and survival of released adult and young ferrets.

Methods

Stratification Based on Rearing and Prerelease Experience

Rearing conditions and prerelease experience have profound effects on behaviors of young ferrets (Miller and

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others, 1990a,b; Vargas, 1994; Biggins and others, 1999; Biggins, 2000), ultimately influencing postrelease survival rates (Biggins and others, 1998). Released adult (age at release >1 year) black-footed ferrets reported herein were given experience in outdoor pens, including living in natural burrows and killing prairie dogs, for 1–4 months prior to release. Former experimental designs that focused on testing effects of rearing on young ferrets (kits), however, involved more categories of preconditioning and more carefully controlled environments (Biggins and others, 1998). Those experimental designs encompassed most of the radio-tagged kits used in the following analyses but only a portion of the released kits that were not telemetrically monitored. Because early experiments indicated that cage-reared kits were dramatically different in several respects from their counterparts with experience in pens (Biggins and others, 1998, 1999), we did not include cage-reared kits in any of our analyses (telemetry or recapture). We also excluded kits that were born in pens or transferred into pens at the natal facility at an early age (<60 days) with their dams (the PENRES category of Biggins and others, 1998) from the telemetric data set. For a large number of kits that were not part of the early experiments, preconditioning was much more variable. Thus, our capture-recapture analyses encompassed a more broadly defined "preconditioned" group of kits that ranged from those placed in pens prior to 60 days of age with dams to those shipped after 90 days of age, without accompanying adults, from their original breeding facility to pens at other facilities or to remote pens near reintroduction sites.

In summary, we used two types of data to examine the influence of age of ferrets on their movements and survival. Radio telemetry provided information on cumulative movements, dispersal, minimum survival rates, and causes of mortality. A larger sample of ferrets that were individually marked (including those that were radio tagged) allowed additional estimates of survival via mark-recapture methods.

Radio Telemetry

We radio collared 137 black-footed ferrets with 5-g transmitter packages attached to 100 percent wool collars with Teflon® (DuPont, Wilmington, Del.) heat-shrink tubing (the latter to resist mud accumulation). Radio-tagged ferrets were released on Gunnison's prairie dog (*Cynomys gunnisoni*) habitat in the Aubrey Valley of northern Arizona and on black-tailed prairie dog (*C. ludovicianus*) habitat at UL Bend National Wildlife Refuge in Montana and the Burns Basin portion of Badlands National Park, S. Dak.

Transmitters, with their 20-cm whip antennas, provided a pulsed signal (pulse interval = 1.5 seconds; pulse width = 20 milliseconds) of about -14 dB, with battery life of about 45 days. Radio location was accomplished via triangulation from fixed stations fitted with paired, 11-element Yagi antennas on rotating masts (Biggins and others, 1999; Biggins, Godbey, Miller, and Hanebury, this volume). We tested accuracy of stations by comparing station-derived azimuths with true azimuths to beacon transmitters. We used standard deviations of the differences between such pairs in confidence intervals to predict the accuracy of future azimuths and the areas and diagonals of error quadrangles associated with positional "fixes" (White and Garrot, 1990). An initial test for each station provided data for evaluating bias patterns and developing formulas for adjustment, and a second set of readings was used to calculate residual variation after bearings were adjusted (Biggins and others, 1999). We referenced stations prior to each tracking session (Biggins, Godbey, Miller, and Hanebury, this volume) using from 2 to 5 beacon transmitters. For these analyses, we used radio-telemetry data for the first 14 days postrelease (although tracking extended over a longer period at some sites). We used the computer program TRITEL to process azimuth data (Biggins, Godbey, Miller, and Hanebury, this volume); processing included adjustments for referencing and bias and calculation of coordinates and error estimates for each fix. Hand-held tracking equipment assisted us in recovery of lost collars and dead ferrets.

For comparisons of age groups, we used the subset of the 137 instrumented animals (excluding 20 PENRES kits and 23 cage-reared kits as defined above) that included 38 adults and 56 "preconditioned" kits (table 1). We screened data for gross radio-tracking and data entry errors by using the systematic approach of Breck and Biggins (1997). We then summarized cumulative movements between consecutive fixes and dispersal from the release site for each ferret and night. We analyzed cumulative movements by using a repeated measures multivariate general linear model (MGLM) with average area of error quadrangle, sex, and site as covariates. We used square root transformations of the response variables to improve normality and homoscedasticity of residual variation. We assumed that the area of an error quadrangle would account for a portion of the variation in the cumulative movement of a ferret and retained this measure of tracking error as a control variable in statistical models regardless of its significance. Because dispersal is defined as movement away from the release site and increased distance from tracking stations causes larger error quadrangles, tracking error was not considered in statistical evaluations of dispersal, but sex and site were included as covariates.

Causes of mortality were determined by evidence at recovery sites (e.g., tracks, scat, fur, feathers, digging), condition of carcass (e.g., hemorrhage, bite wounds, saliva), and radio-tracking data (patterns of fixes and activity, timing of death). We assessed risk-adjusted survival rates by relating deaths (table 1) to days of telemetric monitoring (Heisey and Fuller, 1985). An estimate of maximum survival resulted from considering only known deaths. Counts of animals known dead underestimate mortality rates because not all dead animals are detectable (underground deaths due to badgers, for example, may be underestimated) and because some proportion of loss of telemetric contact with animals is due to transmitter damage inflicted during predation. (We have recovered a few badly damaged transmitters that were barely functional and assume that others became nonfunctional.) We thus

Table 1. Numbers of preconditioned adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) released in Arizona, South Dakota, and Montana during 1994–96.

	Arizona (1996)	South Dakota (1995–96)	Montana (1994)	Montana (1995)	Total
Ferrets					
Adult	15	14	5	4	38
Kit	8	11	10	27	56
Total	23	25	15	31	94
Ferret-days of monitoring					
Adult	90.7	21.3	25.0	29.7	166.7
Kit	43.0	93.2	54.0	291.0	481.2
Total	133.7	114.5	79.0	320.7	647.9
Deaths					
Adult	4	11	3	1	19
Kit	0	5	5	1	11
Total	4	16	8	2	30

estimated a minimum survival rate by summing the number of ferrets that were lost from telemetric contact and the number known to be dead. If an animal was found alive at a later date during spotlight surveys, it was considered alive for the first 14 days (even if telemetric contact was lost and it would have been listed as missing). If an animal died or became missing after 14 days, it was treated as alive for the first 14 days. Our multivariate general model had eight parameters (two ages, four site/year combinations). In this survival analysis, we compared models and their nested submodels using likelihood ratio tests.

Table 2. Numbers of preconditioned adult and young black-footed ferrets (*Mustela nigripes*) marked and released at sites in Montana, South Dakota, and Utah-Colorado during 1994–2001.

	South Dakota (1994–2000)	Montana (1994–97)	Utah-Colorado (1999–2001)	Total
Adult	49	13	60	122
Kit	261	80	160	501
Total	310	93	220	623

Mark-recapture

The data set for this portion of the study (table 2) included all black-footed ferrets released during 1994–2000 at Badlands National Park and Conata Basin in South Dakota, ferrets released during 1994–97 at UL Bend in Montana (including the radio-tagged individuals mentioned above), and ferrets released at the Coyote Basin site of Utah and adjacent Colorado. Of the 623 ferrets released (table 2), 325 were males and 298 were females. All released ferrets were individually marked, mostly with passive integrated transponder (PIT) tags subcutaneously implanted over the shoulder. A second PIT tag often was implanted over the hip (Biggins, Godbey, Matchett, and others, this volume). "Recapture" (in this case, mostly reading the transponder) was accomplished via spotlight surveys to locate the ferrets (Campbell and others, 1985; Biggins and others, 1998) followed by placement of a transponder reader at the occupied burrow to automatically read and retain the chip number (Biggins, Godbey, Matchett, and others, this volume). The first survey at each site usually was conducted about 1 month postrelease, with additional surveys conducted prior to the breeding season (in some cases) and postwhelping (most sites). Intensity of these survey efforts varied among sites and years due to availability of resources.

Counts of surviving animals at 30 and 150 days postrelease were based on the same released ferrets and thus cannot be considered statistically independent. Also, the 71 radio-tagged ferrets in South Dakota and Montana are a subset of the 623 animals considered in the capture-recapture analyses. We chose to maintain separate 30-day and 150-day mark-recapture analyses (rather than a more complex single model) because of sample size differences and unequal time intervals between surveys and because survival estimates for these time periods can be compared with similar estimates reported elsewhere for ferrets. Survival was considered cumulatively; ferrets found alive at 150 days (or later) were counted as alive on day 30 even if they were not found in the earlier period. Because spotlight sessions of equal intensity were not replicated systematically at all sites (or even among days within sites), we did not attempt traditional capture-recapture modeling where capture rates and survival rates could be estimated separately. Our rates, therefore, must be considered as minimum survival (the products of capture rate and survival rate), recognizing that not all ferrets were likely to have been located at any site. Interpretation of the comparisons between adults and kits thus requires the assumption that each age class (within each site) was equally detectable by spotlighting, an assumption that we believe is reasonable. We estimated survival rates from spotlight searches by using an iterative numerical optimization procedure (program SURVIV; White, 1983). The general model included 12 parameters (3 sites, 2 sexes, 2 ages).

Elapsed time from release until the last detection for each ferret also was calculated. Time intervals between releases and the first spotlight survey and between subsequent spotlight surveys varied considerably among sites and years, from a single survey per year to nearly continuous surveys. Variability in survey timing tended to distribute this measure of survival in a continuous (but skewed) form, and square root transformation improved its suitability for use as a continuous response variable in a MGLM analysis, allowing additional assessment of the potential interaction between age and sex.

We recognize that detectability of ferrets via spotlight searches is likely to differ among sites due to differences in access, vegetative cover, topography, intensity of effort, and other variables. Thus, we consider multivariate modeling, with a site variable included, as critically important. Potential differences in search efficiency also preclude any conclusions regarding differences in survival among sites.

An important consideration in our experimental design, for both telemetric and capture-recapture data, was to maintain a reasonable balance of treatments within sites (and within years, with one exception). Other priorities always affected allocations of animals, but, to avoid serious confounding during interpretation of results, we did not allow any cell of the design to be empty. Thus, groups of released ferrets that did not contain adults and kits of both sexes were excluded from analyses. The exception to this general rule occurred within the telemetry data set, where adult ferrets were released in Badlands National Park in spring, and kits were released at that site during fall of the following year.

We followed the principle of parsimony in evaluating competing statistical models (Lebreton and others, 1992), attempting to reduce general models to simpler submodels by eliminating variables that appeared to have low explanatory power. For capture-recapture analysis within program SURVIV, reduced models were evaluated by likelihood ratio tests and Akaike's Information Criterion (AIC) (Anderson and Burnham, 1994). For MGLM evaluations and likelihood ratio testing, *P* values >0.10 were deemed sufficient for eliminating variables from models.

Results

Radio Telemetry

Of the 137 radio-tagged ferrets that were released, 59 were considered lost to the population, mostly as a result of predation (fig. 1). Coyotes (*Canis latrans*) caused the most losses, but prior to its removal a great horned owl (*Bubo virginianus*) had a substantial impact at one site in South Dakota. American badgers (*Taxidea taxus*) were common on prairie dog colonies where ferrets were released, but they killed ferrets only occasionally. The species of predator responsible for ferret deaths could not always be determined, however, resulting in some classifications of "unknown predator" or "unknown raptor" (fig. 1).

Multivariate repeated measures analysis of square root transformed cumulative movements for ferrets that were monitored for at least three nights yielded a significant interaction between night postrelease and age group ($F_{2,59} = 7.407$, $P = 0.001$) with a model that included age, site, and mean area of error quadrangle (per animal over three nights). Thus, the pattern of change in nightly movements of kits and adults was significantly different over the first three nights postrelease (fig. 2; nontransformed data). Tracking error (area of error quadrangle) contributed significantly to the variation in movements ($F_{1,60} = 5.620$, $P = 0.021$), underscoring the importance of a variable to account for this source of "nuisance" variation

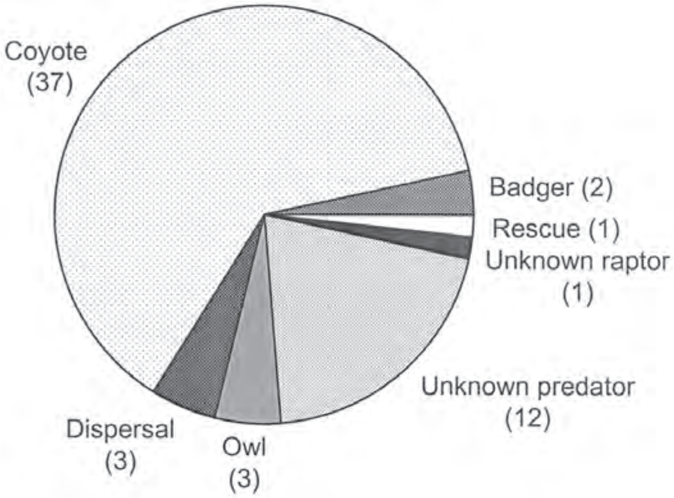

Figure 1. Causes of loss for 59 of 137 radio-tagged black-footed ferrets (*Mustela nigripes*) released in Montana, South Dakota, and Arizona during 1994–96. "Rescued" ferrets are those that we assume would have been lost without our intervention (translocation or treatment for injuries). "Unknown predator" and "Unknown raptor" are general categories for which the species of predator could not be identified.

in models of movement. Nightly movements also appeared to be different at different sites ($F_{3,60} = 3.693$, $P = 0.017$).

The relatively long movements of adult ferrets on the night of release suggested that they might have “bolted” from the release site (i.e., dispersed rapidly away from the point of release), but a repeated measures analysis of dispersal during the first three nights did not support that contention (fig. 3). Although there was a significant tendency for ferrets to drift away from their release sites over the first several nights ($F_{2,58} = 8.860$, $P < 0.001$), the pattern of dispersal was not significantly different for kits and adults ($F_{2,58} = 1.107$, $P = 0.337$). Thus, “bolting” is not an appropriate description of the behaviors of adults. They simply moved more than kits during their first night but did not tend to leave the area of release any differently than did kits. In this analysis of dispersal, there was no evidence of differences among sites ($F_{3,59} = 1.209$, $P = 0.315$).

Survival of radio-tagged adults appeared to differ significantly from survival of radio-tagged kits. For the estimates of maximum survival, generated by considering only known deaths (fig. 4), likelihood ratio testing did not support reduction in number of parameters by pooling sites ($X^2 = 45.4$, $df = 6$, $P < 0.001$) or ages ($X^2 = 29.3$, $df = 4$, $P < 0.001$). The same was true for the estimates of minimum survival, using ferrets known to be dead plus those with whom radio contact was lost during the 14-day tracking period (sites, $X^2 = 38.6$, $df = 6$, $P < 0.001$; ages, $X^2 = 38.7$, $df = 4$, $P < 0.001$). There was thus a similar overall pattern of differences between survival rates of adults and kits, regardless of the method of categorizing mortalities (fig. 5). If about one-third of the missing animals actually died when their signals were lost, the overall projected survival rates for 30 days postrelease would have been 42 percent for kits and 11 percent for adults. The curves vary among sites and with methods, but kit survival was higher than adult survival within each comparison.

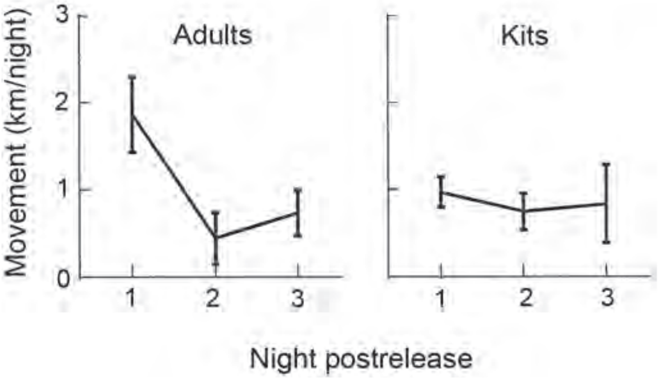

Figure 2. Mean cumulative nightly movements for adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) during the first three nights postrelease (mean ± SE).

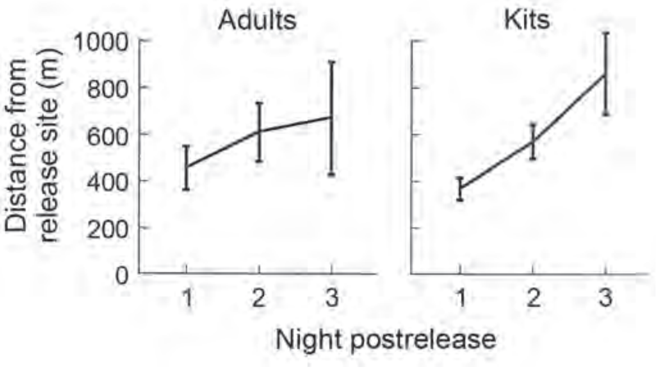

Figure 3. Nightly maximum displacement from release sites for young and adult radio-tagged black-footed ferrets (*Mustela nigripes*) during the first three nights postrelease (mean ± SE).

Mark-recapture

The preferred model of minimum survival from the spotlight search data was the general model for both the short-term (30-day) (table 3) and the long-term (150-day) assessment (table 4), although the evidence for distinction between the sexes was strongest in the long-term evaluation. Minimum survival rates were higher for kits than for adults in 11 of the 12 pairs of estimates for the two time periods, averaging 45.5 percent (kits) and 9.8 percent (adults) at 30 days (fig. 6) and 25.9 percent (kits) and 5.7 percent (adults) at 150 days (fig. 7). Minimum survival rates tended to be higher for females

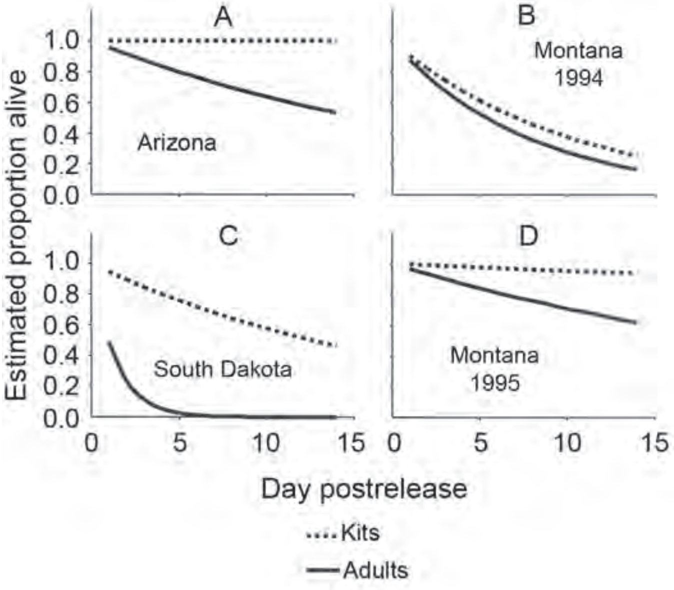

Figure 4. Postrelease survival curves for preconditioned adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) extrapolated from daily survival rates (assuming a constant hazard rate for the 14-day period of the experiment and using only known deaths).

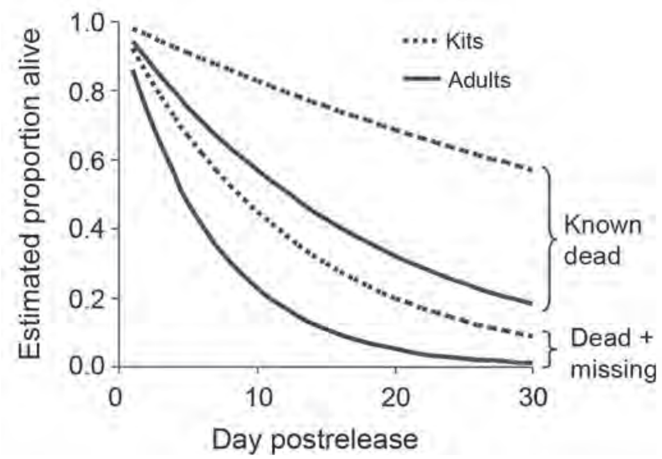

Figure 5. Bracketed high and low survival of adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) for the first 30 days postrelease, generated by using only ferrets known to be dead (high) and known deaths plus ferrets lost to radio contact (low). Curves were extrapolated from daily survival rate estimates assuming a constant hazard rate for the period.

than for males (figs. 6 and 7). For kits, the disparity between sex-specific survival rates was proportionately greater for the long-term estimates (males, 18.9 percent; females, 35.7 percent) than for the short-term estimates (males, 39.9 percent; females, 53.4 percent). Moreover, there seemed to be different patterns for adults and kits within the two genders for both the short-term and long-term data sets. That potential interaction warranted closer examination.

General linear modeling of elapsed time between release and the last detection demonstrated a significant interaction between sex and age ($F_{1,617} = 5.522$, $P = 0.011$); known survival times tended to be shorter for adults than for kits (fig. 8). We retested the sexes separately because of the interaction. As implied by the pairs of graphs, female kits survived significantly longer than did adult females ($F_{1,294} = 40.250$, $P < 0.001$), but the difference between the age groups was only marginally significant for males ($F_{1,294} = 3.387$, $P = 0.067$).

Discussion

Radio Telemetry

There is a potential bias built into assessments of ferret movements. Repeated measures analyses, particularly, require complete sets of multiple measures on single animals; any ferret that lacked a measure of movement for any of the first three nights postrelease (fig. 2), for example, was excluded from our analysis. Thus, ferrets that tend to engage in risky behaviors tend to be removed (by death) at higher rates from the sample, likely causing movements to be generally underestimated, and (more seriously for this kind of experiment) the effect may be greater on some treatment groups than on others. If we assume that there is a positive correlation between movement and mortality rate (Biggins and others, 1998), we likely underestimate movement differences between groups. We have been able to detect such differences, but more subtle disparities between treatment groups may remain unnoticed. Statistical models that are not based on repeated measures also would be affected, but more flexible rules for handling those data should result in a less dramatic influence. Although early deaths of individuals having presumably lower fitness may cause a shift in representation of animals, their movements before they were killed remain in data sets used for statistical analyses other than repeated measures.

Survival of radio-tagged kits differed more dramatically from adults at the Burns Basin, S. Dak., release site than at any other site (fig. 4). Although the same release site was used for both kits and adults, and they were radio tracked from the same system, Burns Basin was the only site where adults and kits were not released at the same time. It is possible that the differences there were due to year or season.

The different appearance of survival curves among sites generated from telemetric data (fig. 4) should not be construed as being linked to the species of prairie dog or other site-specific conditions. Efficiency of radio tracking is likely responsible for much of the variation. The Aubrey Valley site

Table 3. Modeling of short-term (30-day) return rates for preconditioned black-footed ferrets (*Mustela nigripes*) released at three sites, with parameter estimates for sites, sexes, and ages.

Model	ln(L)[a]	np[b]	AIC[c]	Versus model[d]	X^2	*P*
1. General	-19.842	12	63.685			
2. Sites same	-65.391	4	138.783	1	91.10	<0.001
3. Ages same	-53.722	6	119.443	1	67.76	<0.001
4. Sexes same	-28.060	6	68.120	1	16.44	0.012

[a] ln(L) = log-likelihood.

[b] np = number of parameters.

[c] AIC = Akaike's Information Criterion.

[d] The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.

Table 4. Modeling of long-term (150-day) return rates for preconditioned black-footed ferrets (*Mustela nigripes*) released at three sites, with parameter estimates for sites, sexes, and ages.

Model	ln(L)[a]	np[b]	AIC[c]	Versus model[d]	X^2	*P*
1. General	-16.687	12	57.374			
2. Sites same	-34.662	4	77.324	1	35.95	<0.001
3. Ages same	-35.060	6	82.121	1	36.75	<0.001
4. Sexes same	-28.609	6	69.219	1	23.84	0.001

[a] ln(L) = log-likelihood.

[b] np = number of parameters.

[c] AIC = Akaike's Information Criterion.

[d] The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.

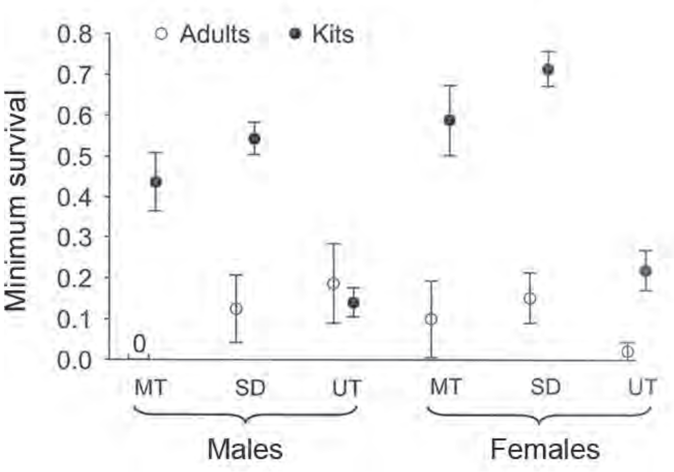

Figure 6. Minimum short-term (30-day) survival of adult and young preconditioned black-footed ferrets (*Mustela nigripes*) released onto prairie dog colonies (*Cynomys* spp.) in Montana (MT), South Dakota (SD), and Utah (UT) during 1994-2001 (mean ± SE).

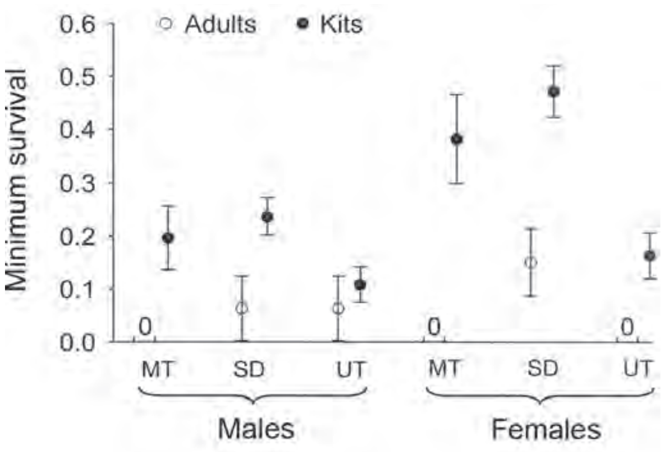

Figure 7. Minimum long-term (150-day) survival of adult and young preconditioned black-footed ferrets (*Mustela nigripes*) released onto prairie dog (*Cynomys* spp.) colonies in Montana (MT), South Dakota (SD), and Utah (UT) during 1994–2001 (mean ± SE).

in Arizona, in particular, presented a challenge. Wide spacing between stations was necessary to achieve appropriate coverage of the site, but contact was lost with many animals because of the long distances over which they were tracked. The result may have been a reduced probability of finding dead ferrets, and such known mortalities were the basis for the curves generated. In contrast, Burns Basin in South Dakota provided much better radio-tracking conditions that favored finding cases of mortality (stations were on high points). Overall, highest rates of survival for kits have been in South Dakota as exemplified by our mark-recapture data set. Site characteristics have influenced the efficiency of both spotlight searches and radio telemetry, causing us to adopt experimental designs that compare two or more treatments within sites, to replicate the design over multiple years and sites to achieve adequate sample sizes, and to exercise caution in interpreting results from multiple sites. We might have remained more suspicious about the possible ramifications of our design and potential for confounding without the corroborating results produced by the much larger sample sizes of released ferrets in the mark-recapture portion of the study.

Mark-recapture

Differences between survival rates of males and females were not detected previously (Biggins and others, 1998) in a much smaller data set of 262 ferrets (64 of those animals were included in our present data), although there was speculation that the expected trend toward lower male survival in longer-term data was developing and would be validated with larger sample sizes. Failure to detect such a difference in our data would indeed have been troubling given the male bias in the numbers of animals released (325 males:298 females) and the female-biased composition of free-ranging ferret populations (Forrest and others, 1988). For kits only (comparable to the analysis of Biggins and others, 1998), a gender effect

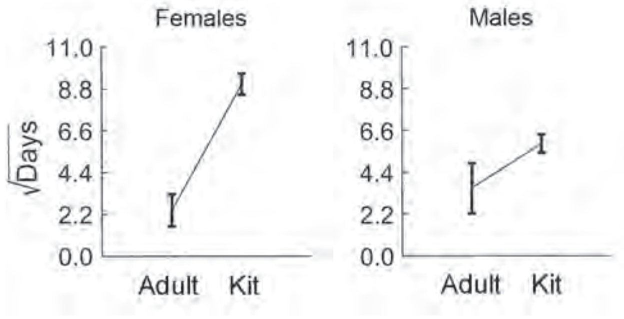

Figure 8. Number of days of known survival for marked adult and young black-footed ferrets (*Mustela nigripes*) calculated using detections from spotlight searches, snow-track searches, and radio telemetry (mean ± SE).

in our data was detectable for both the short-term and long-term evaluations, but the effect became more dramatic over time. Perhaps males became increasingly territorial during the approach of breeding season.

The significant interaction between age and sex classes has potentially nontrivial management ramifications. The interaction may be explained if older age tends to confer greater social status to males than to females, creating a potential problem if adult males have poor long-term survival skills compared to preconditioned male kits. Some older males may be able to competitively exclude younger males, subjecting the latter to temporarily higher mortality. The competition could result in lower overall survival rates for young males without any compensatory increase in long-term survival rates for adult males. If younger males are lost during transitory social interactions with dominant older males, and the older males tend to be lost before breeding season, a shortage of males could result. This phenomenon could occur with concurrent releases of adult and young males, or during releases to augment populations.

General Considerations

Daily survival rates estimated from the 14-day radio-telemetry data set for 94 radio-tagged ferrets seemed reasonably predictive of the 30-day survival rates derived from mark-recapture data on the larger data set of 623 animals. The telemetrically originated survival rates of 42 percent for kits and 11 percent for adults are similar to the overall capture-recapture survival rates of 46 percent for kits and 10 percent for adults. Such comparisons are speculative, however, because of the differing methods and attendant assumptions. First, it is only a reasonable guess to assume that one-third of cases of lost radio contact were due to death of the ferret. Second, the 14-day survival rates were produced under the assumption of a constant hazard rate, an assumption that was repeated to produce the 30-day extrapolation. Hazard rates likely decline postrelease as ferrets with lower fitness are culled and as ferrets learn about their new environment. Over short time spans, the flat hazard rate seems reasonable. Applying a rate generated during the first 2 weeks postrelease to long time spans would be ill-advised. Indeed, our spotlight detections at 150 days (25.9 percent of kits released and 5.7 percent of adults released) were much higher than the respective 3.0 percent and 0.0 percent expectations of the extrapolated daily rates from the first 14 days of radio-tracking data. Third, the mark-recapture estimates are for minimum survival; the actual rate must be somewhat higher assuming we do not count all ferrets present. Finally, the average rates discussed here ignore the implications of statistical modeling, which suggested that rates should be separately estimated for sexes and sites.

Postrelease survival of adult black-footed ferrets might be improved if all young were reared in pens whether they were immediately destined for release or for the captive breeding program. A type of phase-specific learning (Davey, 1989) in which an animal may “imprint” on features of its habitat during a critical period of development has not been investigated for ferrets, but differences in postrelease survival and movements of ferrets as a result of rearing history (Vargas, 1994; Biggins and others, 1998, 1999) arouse suspicion. Even if imprinting is not involved, cultural transmission of important behaviors may be enhanced by a natural environment (Biggins, 2000). Ensuring that each generation has early learning experience in a quasi-natural environment has several potential benefits. Whether or not all kits are raised in pens, increasing the amount of time they spend in outdoor pens could be advantageous. Females that have spent three summers rearing young in the burrows of outdoor pens may make better candidates for release than females without such experience. Perhaps males could be kept in the outdoor pens during much of the remainder of the year, a practice that may accrue additional benefits in reproductive performance (D. Kwiatkowski, oral commun., 1991). Additional investigations of these types of variables might lead to enhanced postrelease survival of captive-reared ferrets.

At this point in the recovery program, black-footed ferret kits seem to have short-term and long-term survival rates at least fourfold higher than those of adult ferrets. On the other hand, ferrets released at age 3 or 4 likely have already exceeded the mean life spans of their wild-born counterparts in established populations. Some female ferrets released as adults have produced litters (in South Dakota and Arizona), and a male released at age 5 in South Dakota survived at least 3.5 years longer, becoming the oldest known ferret in the wild at age 8.5. Such anecdotal information representing extreme cases should carry little weight in decisionmaking, but neither do we presume that data on survival rates for hundreds of ferrets can lead to unequivocal recommendations regarding the advisability of releasing adults. Decisions will need to depend partly on interpreting survival rates of released adults relative to other groups of wild and released ferrets, but philosophical views will continue to exert an influence.

Some conservationists and ethicists may justify extreme means to achieve the goal of preservation and recovery of a species, assuming that the importance of a species is greater than the sum of the rights of its individual constituents (Gunn, 1980). In the words of Rolston (2006, p. 116), “Extinction shuts down the generative processes in a kind of superkilling. It kills forms (species) beyond individuals.” Others may set inviolate moral standards regarding the welfare of individuals wherein the “mere size of the relative population of the species to which a given animal belongs makes no moral difference to the grounds for attributing rights to that individual animal or to the basis for determining when that animal’s rights may be justifiably overridden or protected” (Regan, 2004, p. 360). Even when thinking is focused on the individual ferret, however, opinions differ. Some emphasize the relative safety of a captive ferret; there is little danger it will miss a meal or, worse yet, become one. This line of ethical reasoning could lead to removing each individual “from its predator-filled natural habitat and providing it with a safe, food-rich environment . . . while exterminating the species” (Agar, 1995, p. 403). The controversy over releasing adult ferrets, however, has a narrower focus and seems to stem mostly from differences of opinion over the relative values of longevity and freedom. Remaining in captivity may allow a zoo animal to avoid an “untimely death” (Regan, 2004, p. 396) but prolongs the “harm” (in the form of “deprivation”) that the animal may “suffer as a result of being caged” (Regan, 2004, p. 99). The relative impacts of these “inflictions” and “deprivations” have been contrasted (Regan, 2004, p. 303). Although these philosophical issues may be suitable topics for debate in appropriate forums, extensive discussion of them is beyond the scope of this paper.

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References Cited

Agar, N., 1995, Valuing species and valuing individuals: Environmental Ethics, v. 17, p. 397–415.

Anderson, D.R., and Burnham, K.P., 1994, AIC model selection in overdispersed capture-recapture data: Ecology, v. 75, p. 1780–1793.

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Breck, S.W., and Biggins, D.E., 1997, Detecting and eliminating errors in radio-telemetry data sets—a comparison of screened and unscreened data [abs.], *in* Forum on wildlife telemetry: innovations, evaluations, and research needs: Jamestown, N. Dak., Northern Prairie Wildlife Research Center, U.S. Geological Survey, p. 15.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Davey, G., 1989, Ecological learning theory: London, Routledge, 392 p.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Gunn, A.S., 1980, Why should we care about rare species?: Environmental Ethics, v. 3, p. 17–37.

Heisey, D.M., and Fuller, T.K., 1985, Evaluation of survival and cause-specific mortality rates using telemetry data: Journal of Wildlife Management, v. 49, p. 668–674.

Lebreton, J.D., Burnham, K.P., Clobert, J., and Anderson, D.R., 1992, Modeling survival and testing biological hypotheses using marked animals—a unified approach with case studies: Ecological Monographs, v. 62, p. 67–118.

Miller, B., Biggins, D., Wemmer, C., Powell, R., Calvo, L., and Wharton, T., 1990a, Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*). II. Predator avoidance: Journal of Ethology, v. 8, p. 95–104.

Miller, B., Biggins, D., Wemmer, C., Powell, R., Hanebury, L., Horn, D., and Vargas, A., 1990b, Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*). I. Locating prey: Journal of Ethology, v. 8, p. 89–94.

Regan, T., 2004, The case for animal rights: Los Angeles, University of California Press, 425 p.

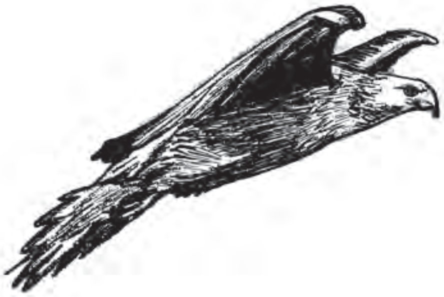
Rolston, H., III, 2006, Our duties to endangered species, *in* Groom, M.J., Meffe, G.K., and Carroll, C.R., eds., Principles of conservation biology (3d ed.): Sunderland, Mass., Sinauer Associates, p. 116-117.

Vargas, A., 1994, Ontogeny of the endangered black-footed ferret (*Mustela nigripes*) and effects of captive upbringing on predatory behavior and post-release survival: Laramie, University of Wyoming, Ph.D. dissertation, 272 p.

White, G.C., 1983, Numerical estimation of survival rates from band-recovery and biotelemetry data: Journal of Wildlife Management, v. 47, p. 716–728.

White, G.C., and Garrot, R.A., 1990, Analysis of wildlife radio-tracking data: San Diego, Calif., Academic Press, 383 p.

Williams, E.S., Thorne, E.T., Kwiatkowski, D.R., Anderson, S.L., and Lutz, K., 1991, Reproductive biology and management of captive black-footed ferrets (*Mustela nigripes*): Zoo Biology, v. 10, p. 383–398.



Does Predator Management Enhance Survival of Reintroduced Black-footed Ferrets?

By Stewart W. Breck,[1] Dean E. Biggins,[2] Travis M. Livieri,[3] Marc R. Matchett,[4] and Valerie Kopcso[5]

Abstract

Predation on black-footed ferrets (*Mustela nigripes*) is a potential problem at reintroduction sites, causing up to 95 percent of the documented mortality of ferrets. Strategies to reduce mortality due to predation can focus on preconditioning ferrets prior to reintroduction and/or managing predators of ferrets. Biologists have tried three general strategies to control predators at reintroduction sites: (1) selective removal of individual predators, (2) nonselective removal of coyotes (*Canis latrans*), and (3) electric fences to exclude coyotes from release sites. We conducted a post hoc review of data from releases during 1994–2003 at 11 sites in South Dakota and Montana to address whether or not predator management has benefited reintroduced black-footed ferrets. Limited evidence indicates that (1) individual great horned owls (*Bubo virginianus*) can cause significant ferret mortality and that identifying and removing these individuals can be beneficial, (2) lethal control of coyotes may have inverse effects on ferret survival, and (3) electric fencing does not enhance short- or long-term survival of reintroduced ferrets. The data are confounded by a variety of factors, making conclusions tenuous. Well designed studies are needed to properly address the effectiveness of predator management for enhancing ferret survival.

Keywords: black-footed ferret, *Bubo virginianus*, *Canis latrans,* coyote, electric fencing, great horned owl, *Mustela nigripes*, predator control

Introduction

Successful recovery of black-footed ferrets (*Mustela nigripes*) will ultimately depend upon our ability to understand and manage a number of ecological factors (e.g., genetic inbreeding, disease, habitat, and predation) that influence survival, reproduction, and recruitment of ferrets in recovering populations. The role of predators in ecology, conservation biology, and wildlife management has gained increasing recognition as a factor to understand and potentially manage (Estes and others, 2001; Terborgh and others, 1999). For ferrets, mammalian and avian predation has been identified as a critical ecological component in both established populations (Forrest and others, 1988) and reintroduction efforts (Biggins and others, 1998; Biggins, 2000; Biggins, Godbey, Livieri, and others, this volume).

For example, at Meeteetse, Wyo., where the ancestral free-ranging population of ferrets was studied, 57 percent of known mortality of wild ferrets was due to predation (Forrest and others, 1988). Predation by great horned owls (*Bubo virginianus*), golden eagles (*Aquila chryseatos*), and coyotes (*Canis latrans*) was recorded, leading Forrest and others (1988) to conclude that in the Meeteetse ferret population: (1) annual mortality was high, (2) few if any ferrets lived to 3+ years, (3) 59 percent to 77 percent of all juveniles disappeared each year (when disease was not present), (4) adults disappeared at a rate about 80 percent of that seen in juveniles, and (5) predation was the most significant cause of ferret mortality (when disease was not present). For reintroduced animals, predation is equally if not more important, accounting for over 95 percent of the ferrets lost from reintroductions (Biggins, 2000; Biggins, Godbey, Livieri, and others, this volume). For those ferrets killed by predators, coyotes accounted for over 60 percent of the mortality and may have accounted for another 20–30 percent of unconfirmed predation. Badgers (*Taxidea taxus*), great horned owls, and other raptors accounted for a small portion of the predation.

A number of factors likely contribute to the dynamics of predator-ferret interactions, including predator density and behavior, availability of alternative prey, habitat conditions, and, for reintroduced animals, the level of preconditioning individuals receive before being released to the wild. Preconditioning enhanced survival of reintroduced ferrets and Sibe-

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rian polecats (*Mustela eversmannii*; Biggins and others, 1991, 1998, 1999). The foregoing research helped lead to establishment of a general preconditioning program for all ferrets released into the wild. Concurrent with the preconditioning research, biologists and managers from different release sites also tried techniques for managing predators to enhance survival of newly released ferrets. Early studies indicated that mortality of surrogate Siberian polecats was higher in areas with more predators (Biggins and others, 1991). Predator management primarily focused on coyotes and included both lethal and nonlethal techniques. Lethal management primarily involved removing coyotes in and around release areas prior to release of ferrets. To a lesser extent badgers and great horned owls were occasionally killed, mostly in attempts to stop individuals that apparently developed a search image for ferrets. In addition to lethal control, many release sites used electrified fencing to exclude terrestrial predators (primarily coyotes and badgers) for short periods (30–60 days postrelease). The results of these management actions have not been synthesized and published outside of internal reports. Our objective here is to explore existing data to determine if lethal coyote control, electric fencing, or selective removal of individual predators enhanced short-term and/or long-term survival of reintroduced black-footed ferrets.

Study Area and Methods

We synthesized data from black-footed ferret reintroduction sites in Montana and South Dakota and only used data on ferrets that had been preconditioned. Although other data were available from releases in Wyoming, Arizona, and Colorado/Utah, differences in prairie dog (*Cynomys*) species, preconditioning of ferrets, detectability of ferrets, and monitoring methodology from these sites precluded their inclusion in this analysis. In Montana a total of 10 releases occurred from 1994 to 2003, and in South Dakota, 10 releases occurred from 1994 to 1999 (table 1). All releases occurred on black-tailed prairie dog (*C. ludovicianus*) colonies, with higher densities of prairie dogs occurring on the South Dakota sites.

For each release, both short-term (30 days postrelease) and long-term (6–8 months postrelease) estimates of survival were determined by spotlighting ferrets (Campbell and others, 1985). Each survival estimate was based on a multiple night effort in which personnel in vehicles and on foot surveyed release areas with spotlights to detect ferrets. Any ferret detected was identified by using an automatic passive integrated transponder (PIT) reader placed at the burrow containing the animal (Biggins, Godbey, Matchett, and others, this volume). Transponders (i.e., PIT tags) were implanted subcutaneously in each individual prior to release. Survival rates were calculated as the percent of ferrets found alive and thus represent minimum survival estimates. Lack of replication in spotlight surveys over short time spans prevented separate estimation of detection rates and survival rates, precluding the use of more sophisticated methods of survival analysis.

We used short- and long-term minimum survival estimates to evaluate whether lethal coyote control and/or electric fencing increased ferret survival. Lethal coyote control was carried out in a variety of ways and intensities across release sites and years. Some release sites were subjected to extensive coyote removal in and around release areas. At other sites smaller numbers of coyotes were removed in conjunction with disease monitoring, and at some sites no coyote removal was performed (table 1). We categorized the level of coyote control as high, medium, or low. High intensity control combined aerial gunning, opportunistic removal onsite, and disease sampling. Medium intensity control combined opportunistic removal onsite and disease sampling in and around the release area. Low intensity effort involved just disease sampling or no lethal control.

Electric fencing (ElectroNet™; Premier1Supplies, Washington, Iowa) was used in attempts to exclude coyotes from some release sites during some years. ElectroNet is 107 cm in height, powered by 12-V deep cycle batteries, and constructed with 10 alternately charged conductors supported with vertical plastic stays every 30 cm. ElectroNet is designed to exclude mammalian species the size of coyotes and badgers while allowing ferrets and other smaller mammals to move through the fence. Experimental trials of ElectroNet excluded coyotes from bait stations for up to 2 weeks (Matchett, 1995), and telemetry data from ferret reintroduction sites indicated that ElectroNet may have enhanced short-term survival of ferrets within fenced enclosures (Matchett, 1999). We tried to extend knowledge of the utility of ElectroNet by testing for differences in both short- and long-term minimum survival between those reintroduction sites that used ElectroNet and those that did not (table 1). The perimeter of fencing used at reintroduction sites varied from 3.5 km to 13 km and was maintained for a minimum of 30 days postrelease.

We hypothesized that ferrets in areas with higher densities of prairie dogs (i.e., South Dakota), higher levels of coyote control, and electric fencing would have higher estimates of both short- and long-term survival. We generated linear models to evaluate this prediction; competing models included interaction terms and combinations of four explanatory variables (see tables 2 and 3 for a complete list of models). We used likelihood-based methods (Buckland and others, 1997; Burnham and Anderson, 1998) to quantify strength of evidence for alternative models explaining patterns of ferret survival. Estimating the “weight,” or probability that a given model is the best approximation to truth among the models considered, is a means for reporting the relative support for alternative models where the weights from the candidate list of models sum to 1. Thus a model with a weight of 1 has complete support and a model with a weight of 0 has no support (Burnham and Anderson, 1998).

We used Proc GENMOD with the logit link option, which assumes a binomial distribution (SAS Institute Inc., 1999) to analyze each model and create output required to

Table 1. Descriptive data on black-footed ferret (*Mustela nigripes*) survival (short-term = 30 days, long-term = 6–8 months) and predator control efforts (high, medium, or low) from 20 release sites in Montana and South Dakota.

Release area and year	Number of ferrets released	Short-term survival	Long-term survival	Number of coyotes removed	Electric fence used?
MT 94	17	0.47	0.41	Medium	No
MT 95	33	0.61	0.33	High	Yes
MT 96	39	0.56	0.15	High	Yes
MT 97	20	0.55	0.20	Medium	Yes
MT 98	21	0.43	0.14	Medium	Yes
MT 99	23	0.35	0.04	Medium	Yes
MT 01 (BLM 40)	20	0.40	0.15	Low	Yes
MT 02 (BLM 40)	25	0.32	0.16	Low	No
MT 03	37	0.76	0.38	Low	No
MT 03 (BLM 40)	20	0.20	missing	Low	No
SD 94	13	0.38	0.23	Medium	No
SD 95	37	0.30	0.08	Medium	No
SD 96 (Agate)	15	0.53	0.07	High	Yes
SD 96 (Burns)	24	0.29	0.13	High	Yes
SD 97 (Kosher)	21	0.76	0.24	Medium	Yes
SD 97 (Sage)	36	0.86	0.69	Medium	Yes
SD 98 (Agate)	25	0.88	0.28	Low	No
SD 98 (Sage)	15	0.73	0.33	Low	No
SD 99 (Hecktable)	36	0.86	0.44	Low	No
SD 99 (Sage)	12	0.75	0.50	Medium	No

calculate Akaike's Information Criterion (AIC) values. We used ferrets as replicates (n = 489) and performed a separate analysis for short- and long-term survival data. For each analysis we assessed the goodness-of-fit by calculating the deviance on the global (fully parameterized) model. We used $\hat{c}$ (deviance/df) to adjust for overdispersion (i.e., lack of fit) and used the small-sample correction of AIC ($QAIC_c$; Lebreton and others, 1992; Burnham and Anderson, 1998) to rank the models and generate an estimate of the weight. We based inferences of survival on the top model.

Results

General patterns in the data show that: (1) both short- and long-term minimum survival estimates have increased in latter years of reintroduction efforts (this was especially true in South Dakota; see table 1); and (2) there was a great deal of variation in estimates of survival across sites and years (short-term low = 20 percent, short-term high = 88 percent; long-term low = 4 percent, long-term high = 69 percent).

Deviance for both global models (short- and long-term analyses) was large (35.5 and 32.7, respectively; $P < 0.001$) indicating that overdispersion was problematic (i.e., fit of model was not good). Based on $QAIC_c$ weights (tables 2 and 3), both short- and long-term minimum survival of reintroduced ferrets were supported by models showing a difference primarily between levels of coyote control and fencing. Ferret survival was inversely related to coyote control with releases that had the highest levels of control showing approximately 12 percent lower minimum survival compared to the lowest levels of control for both short- and long-term analyses (figs. 1 and 2). Evidence of the effectiveness of electric fencing was opposite of what we predicted; ferrets released in areas with fencing showed lower short- and long-term minimum survival than ferrets released in areas without fencing, 3 percent and 5 percent, respectively (figs. 1 and 2). The variable site was not a factor in either analysis, indicating no detectable differences in minimum survival between release sites. There was only weak evidence that survival of ferrets differed between States (i.e., the variable State was part of the 2nd ranked model in the long-term analysis; table 3), indicating differences in prairie dog density between States did not appear to influence survival.

Table 2. Results of the Akaike's Information Criterion (AIC) model selection procedure to determine the model that best explains 1-month survival patterns of reintroduced black-footed ferrets (*Mustela nigripes*), 1994–2003. NPAR is the number of parameters, $QAIC_c$ is a version of AIC adjusted for overdispersion, $DELQAIC_c$ is the difference in QAIC relative to the smallest value in the set, and Weight is an estimate of the likelihood of each model (Burnham and Anderson, 1998). Variables in the models are: fence (present or not), coyote (level of lethal coyote control: low, medium, high), State (Montana or South Dakota), and site (eight different release sites). Dot indicates a model that only includes an intercept (i.e., no explanatory variables). The symbol * indicates an interaction between two variables, and | indicates all possible combinations of the variables.

Model	NPAR	$QAIC_c$	$DELQAIC_c$	Weight
Fence coyote	4	123.41	0.00	0.51
Fence	2	124.93	1.52	0.24
Coyote	3	125.55	2.14	0.18
Dot	1	128.85	5.44	0.03
State fence State*fence	4	129.00	5.59	0.03
Fence coyote fence*coyote	5	132.18	8.77	0.01
State fence	3	133.20	9.79	0.00
State coyote	4	136.25	12.84	0.00
State	2	137.76	14.34	0.00
State fence coyote	5	139.17	15.76	0.00
State coyote State*coyote	6	166.83	43.42	0.00
State|fence State|coyote fence|coyote	9	222.85	99.44	0.00
Site	8	346.79	223.38	0.00

Table 3. Results of the Akaike's Information Criterion (AIC) model selection procedure to determine the model that best explains long-term (6–8 months) survival patterns of reintroduced black-footed ferrets (*Mustela nigripes*), 1994–2003. NPAR is the number of parameters, $QAIC_c$ is a version of AIC adjusted for overdispersion, $DELQAIC_c$ is the difference in QAIC relative to the smallest value in the set, and Weight is an estimate of the likelihood of each model (Burnham and Anderson, 1998). Variables in the models are: fence (present or not), coyote (level of lethal coyote control: low, medium, high), State (Montana or South Dakota), and site (eight different release sites). Dot indicates a model with only an intercept (i.e., no explanatory variables). The symbol * indicates an interaction between two variables, and | indicates all possible combinations of the variables.

Model	NPAR	$QAIC_c$	$DELQAIC_c$	Weight
Fence coyote	4	130.67	0.00	0.484
State fence coyote	5	132.98	2.30	0.153
Fence coyote fence*coyote	5	133.16	2.48	0.140
Fence	2	134.31	3.64	0.078
Coyote	3	135.39	4.72	0.046
State fence	3	135.47	4.80	0.044
Dot	1	136.68	6.00	0.024
State coyote	4	138.84	6.17	0.022
State	2	139.60	8.93	0.006
State fence State*fence	4	140.79	10.12	0.003
State coyote State*coyote	6	143.15	12.47	0.001
State|fence State|coyote fence|coyote	9	193.08	62.41	0.000
Site	8	227.04	96.37	0.000

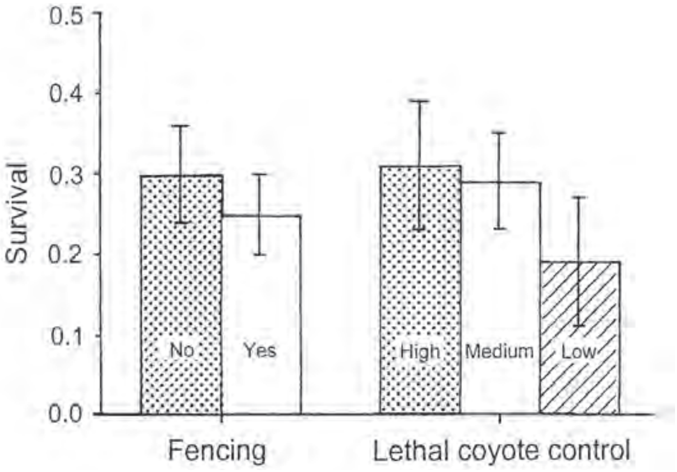


Figure 1. Estimates of short-term (1 month) minimum survival of reintroduced black-footed ferrets (*Mustela nigripes*) for two explanatory variables: fencing (present or not) and lethal coyote control (low, medium, and high). In total, 489 ferrets were released from different sites in Montana and South Dakota from 1994 to 2003. Error bars represent 95% confidence intervals.

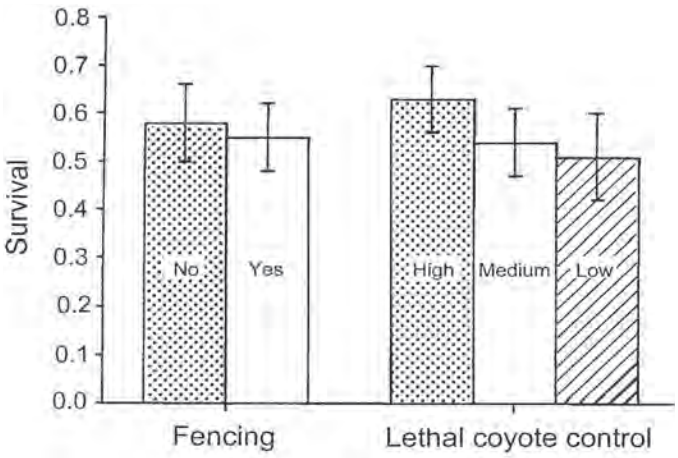


Figure 2. Estimates of long-term (6–8 months) minimum survival of reintroduced black-footed ferrets (*Mustela nigripes*) for two explanatory variables: fencing (present or not) and lethal coyote control (low, medium, and high). In total, 489 ferrets were released from different sites in Montana and South Dakota from 1994 to 2003. Error bars represent 95% confidence intervals.

Discussion

A general pattern that emerged from the data was that estimates of both short- and long-term survival were highly variable even in later years of releases. Variation in survival could be due to a number of factors, including differences in habitat quality, random variation, measurement error, and differences in predation pressure. One factor relating to predators that may have contributed to variation in survival estimates is the role of one or a few problem individuals. Here we define problem individuals as predators that seem to develop a search image for ferrets, consequently becoming disproportionately more successful than other predators at finding and killing ferrets. Critical to the discussion of problem individuals is the realization that mortality of single animals has a larger effect in small populations than in larger populations (Krebs and others, 1995; Krebs, 1996). Thus, it is possible for one or a few individual predators to have a large overall effect on a small population of reintroduced ferrets. A likely example of problem individuals was seen in South Dakota during the 1996 releases (table 1). Nearly half (11 of 24) of the known mortalities that occurred during that release season were caused by one to three great horned owls. In response to the identified problem, three great horned owls were killed on and around the release site, and no further known mortalities were caused by owls. Problem individuals could explain the pattern observed in Montana in 2003 where one release site had a high short-term survival rate of 76 percent while the other had short-term survival of 20 percent, even though no predation by owls was observed.

Our analyses indicated that the relationship between the level of lethal coyote control and ferret survival was opposite of what we hypothesized; that is, more intensive efforts to remove coyotes related to poorer survival for ferrets. This relationship was apparent for both short- and long-term data (figs. 1 and 2). However, several factors are important to consider before drawing any conclusions regarding these patterns. First, most of the high-level efforts for controlling coyotes occurred in earlier years of releases. Thus, the general increase in estimates of survival over time could reflect improvements in preconditioning of ferrets rather than changes in coyote control. Although no data exist to quantify the "quality" of ferrets released over time, it seems possible that preconditioning programs could have improved as the programs were optimized. Second, our method for categorizing levels of coyote control was not ideal. If future research addresses this question, then quantifying density of coyotes pre- and postremoval would be paramount for relating coyote control to ferret survival. Third, increasing survival over successive years may be an artifact of increasing observer efficiency at detecting ferrets or other factors related to estimating survival. The fundamental problem that gives rise to interpretative difficulties mentioned in factors 1–3 previously (and others) is the unbalanced design. All treatments were not replicated at all sites and certainly not in all years at all sites. For example, the BLM 40 complex had only "low" predator control for all 3 years that ferrets were released. Site-specific impacts of unmeasured factors (e.g., disease) may be misinterpreted as treatment effects. Finally, some of the confusion regarding the effectiveness of predator management stems from poor understanding of coyote ecology and behavior in and around release sites. Almost no reliable information exists on activity patterns, use of prairie dog habitat by coyotes, and response of coyotes to control efforts as it relates to black-footed ferrets.

Nevertheless, it is interesting to speculate on how higher levels of coyote control could cause a decrease in ferret survival. Assuming that killing coyotes creates voids filled by coyotes from surrounding territories, one possibility is that as new individuals begin to establish territories, their movements and behavior enhance the probability of encountering ferrets. Many of the ferrets that have been found killed by coyotes were not eaten, indicating that the interaction between coyotes and ferrets may more accurately be described as a form of competition (i.e., intraguild predation; Holt and Polis, 1997; Palomares and Caro, 1999). In competitive interactions, individual animals may not develop specific search images for competitors but rather respond to competitors in an opportunistic fashion. Creating situations in which coyotes are more active (i.e., filling voids) may enhance encounter rates and create greater threat for ferrets.

Of the tools used to control coyote predation, electric fencing offered the most potential to completely eliminate coyote predation on ferrets. The general impression from biologists working at release sites was that fencing did exclude coyotes. At minimum we expected to see higher short-term survival rates for ferrets at sites that used fencing. We found no evidence, however, that fencing enhanced ferret survival for the short- or long-term; in fact, we detected slightly lower survival rates (figs. 1 and 2) at sites that used fencing. Again we caution against strong interpretation of these data for reasons already mentioned, but a couple of factors may explain this pattern.

First, fencing was only used during earlier years of reintroductions (table 1). Though we tried to control for preconditioning in this analysis, it is possible that ferrets released in later years had better preconditioning that enhanced their survival. Second, we know great horned owl predation had a large effect on survival of ferrets at two sites (Agate and Burns) in South Dakota in 1996, both sites that used fencing. Fencing does not deter avian predation, and in this analysis we were unable to control for owl or other avian predation. If we could have controlled for avian predation, it is possible that we would have detected higher survival of ferrets released in areas with fencing, at least for the short-term. Finally, in years when fencing was used, anecdotal observations indicate that many of the ferrets killed by coyotes occurred when ferrets moved outside the fence boundary. Again we were unable to control for this confounding factor in this analysis.

Our results highlight the need to perform well designed experiments to better elucidate the possible benefit of predator management to enhance black-footed ferret survival at reintroduction sites. The fact that survival of reintroduced ferrets remains highly variable indicates that factors other than preconditioning are important. Based on our understanding of ferret ecology, it is likely that predation is responsible for most of the mortality. Understanding whether or not we can manage this predation pressure remains an important goal for ferret recovery. Equally important to recovery efforts is the need to understand the role that predation plays in established populations of black-footed ferrets. Such data would not only provide direct benefits to ferret conservation by potentially increasing the number of ferrets that could be translocated but would also provide better parameter estimates for modeling exercises that depend upon understanding the role of important ecological forces. The most effective means for determining the role of predation in ferret demography and ecology would be to manipulate predator populations and compare responses to unmanipulated populations. Because coyotes are the most important predator of ferrets, we suggest using electric fencing to exclude coyotes as it offers the most potential to control coyote predation.

For the manager who must decide whether or not to manage predators in and around reintroduction sites, we offer the following recommendations. First, great horned owls view ferrets as prey and probably can develop a search image for ferrets. Problem individuals may have large impacts on a population of reintroduced ferrets. If great horned owls are present in the immediate vicinity of a release area, it may be wise to remove individual owls, and, if possible, remove perch sites as well. Second, there is no evidence that lethal removal of coyotes at the levels of control implemented in previous releases enhances short- or long-term survival of ferrets. Extensive control efforts may eliminate coyotes from release sites, temporarily reducing predation pressure on ferrets. However, rates of recolonization by coyotes after such removal are poorly understood and may have important implications for ferrets. Lethal removal of a few individual coyotes probably will not enhance ferret survival because coyotes are often abundant and possibly because of the way coyotes and ferrets interact. Last, electric fencing appears to be an effective method for excluding coyotes and may offer benefits for reintroduced ferrets as long as the fencing is up and functioning. However, maintaining fencing over the long-term is difficult and expensive; thus, fencing is generally only used for short periods (1–2 months). Once fencing is removed, there is no evidence to suggest that the short-term benefits translate into enhanced long-term survival. Thus, for future reintroductions we do not recommend fencing unless the manager can maintain it for long periods or identify how short-term protection may aid long-term survival of ferrets.

References Cited

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 184 p.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Hanebury, L.R., and Miller, B.J., 1991, Trial release of Siberian polecats (*Mustela eversmanni*): Fort Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 25 p.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Buckland, S.T., Burnham, K.P., and Augustin, N.H., 1997, Model selection—an integral part of inference: Biometrics, v. 53, p. 603–618.

Burnham, K.P., and Anderson, D.R., 1998, Model selection and inference—a practical information-theoretic approach: New York, Springer-Verlag, 353 p.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Estes, J., Crooks, K., and Holt, R., 2001, Ecological role of predators, *in* Levin, S.A., ed., Encyclopedia of biodiversity: San Diego, Calif., Academic Press, p. 857–878.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Holt, R.D., and Polis, G.A., 1997, A theoretical framework for intraguild predation: American Naturalist, v. 149, p. 745–764.

Krebs, C.J., Boonstra, R., and Kenney, A.J., 1995, Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada: Oecologia, v. 103, p. 481–489.

Krebs, C.J., 1996, Population cycles revisited: Journal of Mammalogy, v. 77, p. 8–24.

Lebreton, J.D., Burnham, K.P., Colbert, J., and Anderson, D.R., 1992, Modeling survival and testing biological hypotheses using marked animals—a unified approach with case studies: Ecological Monographs, v. 62, p. 67–118.

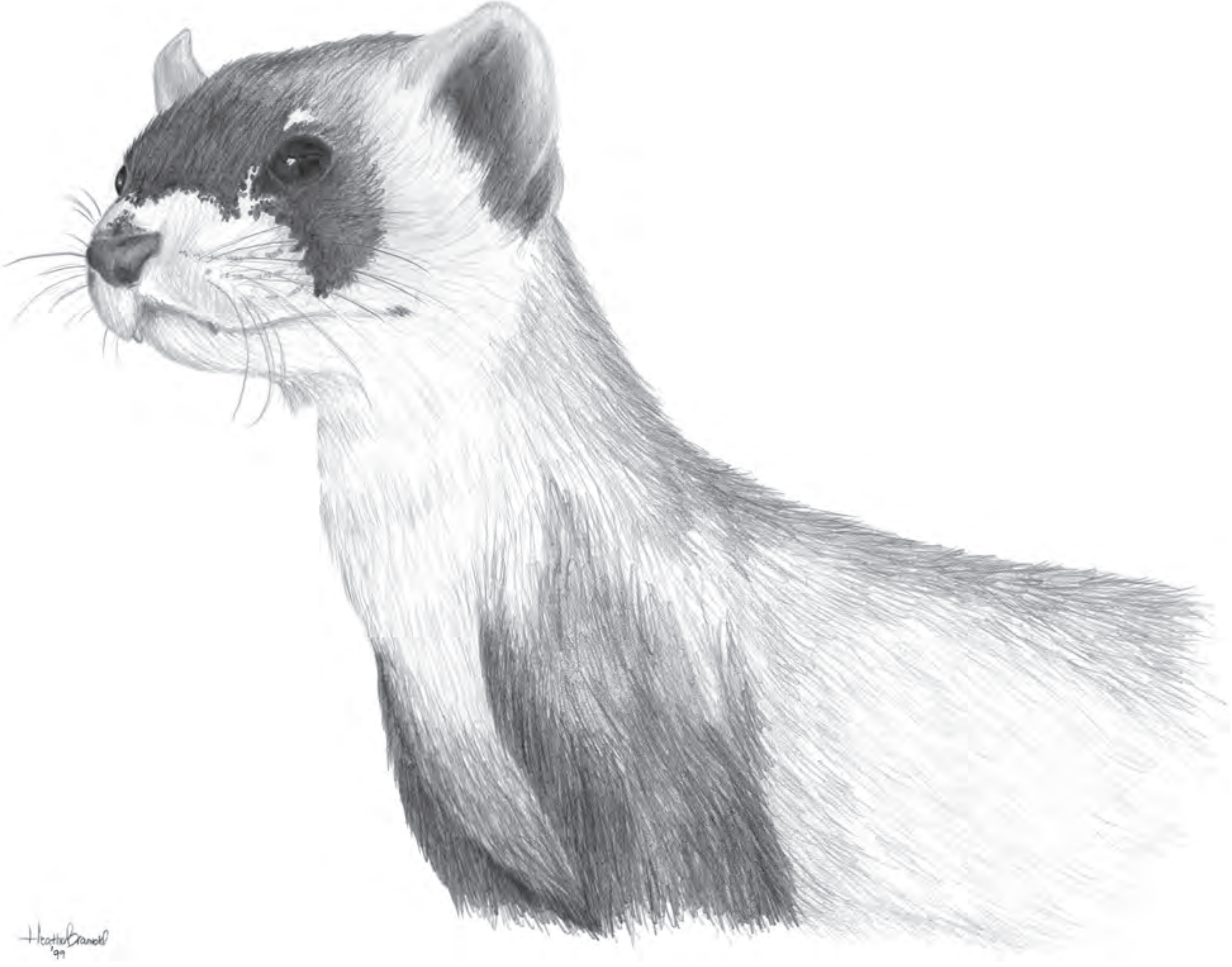
Matchett, M.R., 1995, Trials of electronet fencing to exclude coyotes: Lewistown, Mont., U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, 7 p.

Matchett, M.R., 1999, Black-footed ferret recovery activities on the UL Bend and Charles M. Russell National Wildlife Refuges, Phillips County, Montana—1998 annual report and 5-year summary: Lewistown, Mont., U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, 22 p.

Palomares, F., and Caro, T.M., 1999, Interspecific killing among mammalian carnivores: American Naturalist, v. 153, p. 492–508.

SAS Institute Inc., 1999, SAS OnlineDoc®, Version 8: Cary, N.C., SAS Institute Inc.

Terborgh, J.J., Estes, J.A., Paquet, P.C., Ralls, K., Boyd-Heger, D., Miller, D., and Noss, R., 1999, The role of top carnivores in regulating terrestrial ecosystems, *in* Soulé, M.E., and Terborgh, J., eds., Continental conservation—scientific foundations of regional reserve networks: Washington, D.C., Island Press, p. 39–64.


Heather Branold
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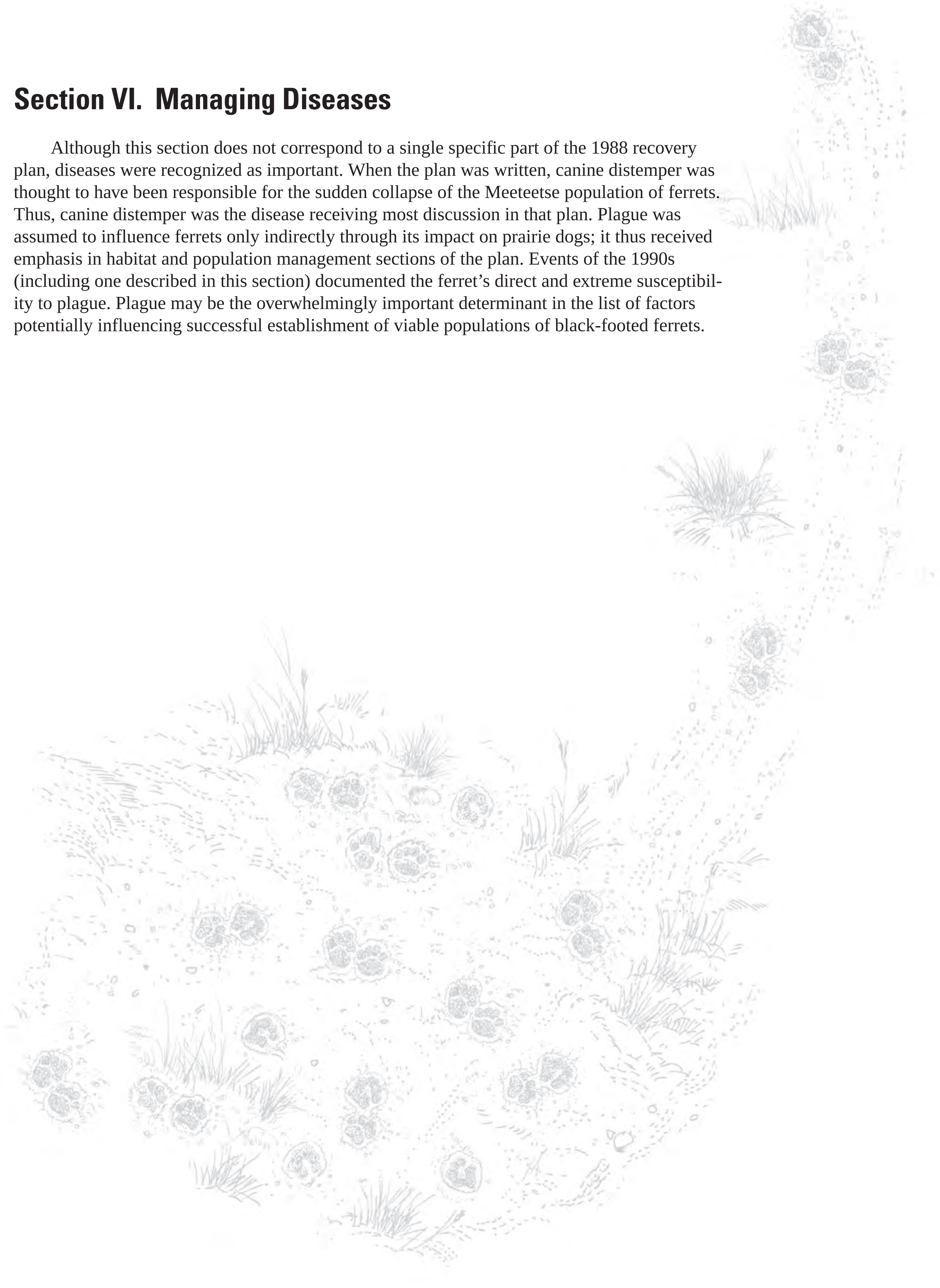
Section VI. Managing Diseases

Although this section does not correspond to a single specific part of the 1988 recovery plan, diseases were recognized as important. When the plan was written, canine distemper was thought to have been responsible for the sudden collapse of the Meeteetse population of ferrets. Thus, canine distemper was the disease receiving most discussion in that plan. Plague was assumed to influence ferrets only indirectly through its impact on prairie dogs; it thus received emphasis in habitat and population management sections of the plan. Events of the 1990s (including one described in this section) documented the ferret's direct and extreme susceptibility to plague. Plague may be the overwhelmingly important determinant in the list of factors potentially influencing successful establishment of viable populations of black-footed ferrets.



Recent Trends in Plague Ecology

By Kenneth L. Gage[1] and Michael Y. Kosoy[1]

Abstract

Plague (*Yersinia pestis* infection) presents serious risks not only to humans but also to wildlife species such as prairie dogs (*Cynomys* spp.) and the critically endangered black-footed ferret (*Mustela nigripes*). The effects of plague are sufficiently serious to hamper recovery of ferrets and prairie dogs in areas that experience repeated epizootic activity. In order to more effectively manage and reduce plague risks for both wildlife and humans, we must improve our understanding of what factors influence the distribution of plague, the transmission and spread of epizootics, and the ability of the plague bacterium to maintain itself indefinitely in some populations of rodent hosts and their flea (Insecta: Siphonaptera) vectors. This article provides a review of our current knowledge of plague ecology. We also describe how recent research advances are providing significant new knowledge and methodologies that can help us better manage plague risks and reduce the impact of the disease on mammalian populations, including those of conservation interest.

Keywords: disease ecology, flea, plague, rodent, *Yersinia pestis*, zoonosis

Introduction

Plague is a flea-borne zoonotic disease caused by the bacterium *Yersinia pestis* (Gage, 1998). The disease is best known as the cause of devastating pandemics, including the Black Death of the Middle Ages. These same pandemics, as well as other more regional outbreaks, also provide striking demonstrations of plague's ability to spread rapidly across vast geographic areas, a process that occasionally results in the establishment of long-term foci of infection among suitable populations of susceptible mammalian hosts and competent flea vectors. At present, active plague foci are found in many countries in Asia, Africa, and the Americas (Gage, 1998; Tikhomirov, 1999; World Health Organization, 2004). In the United States, evidence of plague infection has been identified during recent decades in mammals or fleas in 17 western States (fig. 1).

Although most evidence suggests that virtually any mammal exposed to *Y. pestis* is likely to become infected, the true vertebrate hosts are certain species of rodents (Pollitzer and Meyer, 1961; Gage and Kosoy, 2005). Plague-related mortality can vary greatly between rodent species and even among populations within the same species. In some rodent species mortality approaches 100 percent (Poland and Barnes, 1979). Although certain other rodents appear to be more resistant to plague, even supposedly resistant populations can experience mortality rates in excess of 40 percent (Rivkus and others, 1973). Mortality can also be high among various nonrodent species found naturally infected with *Y. pestis*. Wild and domestic felines, as well as some lagomorphs (hares, rabbits, and pikas), are extremely susceptible (Gage and others, 1994; Gage and Kosoy, 2005). Identification of high seropositivity rates among other nonrodent species, such as coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and feral hogs (*Sus scrofa*), suggests that these species are at least moderately resistant to plague-related mortality (Gage and others, 1994). While most nonrodent species, with the exception of a few lagomorphs and the house shrew (*Suncus murinus*) of southeastern Asia and Madagascar, are not significant hosts of plague, certain mammalian predators and birds of prey probably play important ecological roles by transporting infected fleas from one region to another (Gage and others, 1994).

Elton's (1958) classic book on the ecology of invasions mentions plague as an example of an agent that can spread explosively across vast areas, infecting not only commensal rats (*Rattus* spp.) and "wild" rodents but also other mammals, including humans (Gage and others, 1995; Gage and Kosoy, 2005). Within the past two decades, an increasing number of biologists have become aware of the devastating effects plague has on certain mammal species of conservation interest (Biggins and Kosoy, 2001a,b). Mortality among infected black-tailed prairie dogs (*Cynomys ludovicianus*) reportedly approaches 100 percent during epizootics, and other prairie dog species (*Cynomys* spp.) also are quite vulnerable to the disease (Kartman and others, 1962; Lechleitner and others, 1962, 1968; Rayor, 1985; Ubico and others, 1988; Anderson and Williams, 1997; Cully, 1997; Cully and others, 1997, 2000; Girard and others, 2004; Stapp and others, 2004). Recent evidence also indicates that plague epizootics can cause significant reductions in genetic diversity among prairie dog populations (Trudeau and others, 2004). In some situations plague has both direct and indirect impacts on wildlife populations. Prairie dogs and their endangered predator, the

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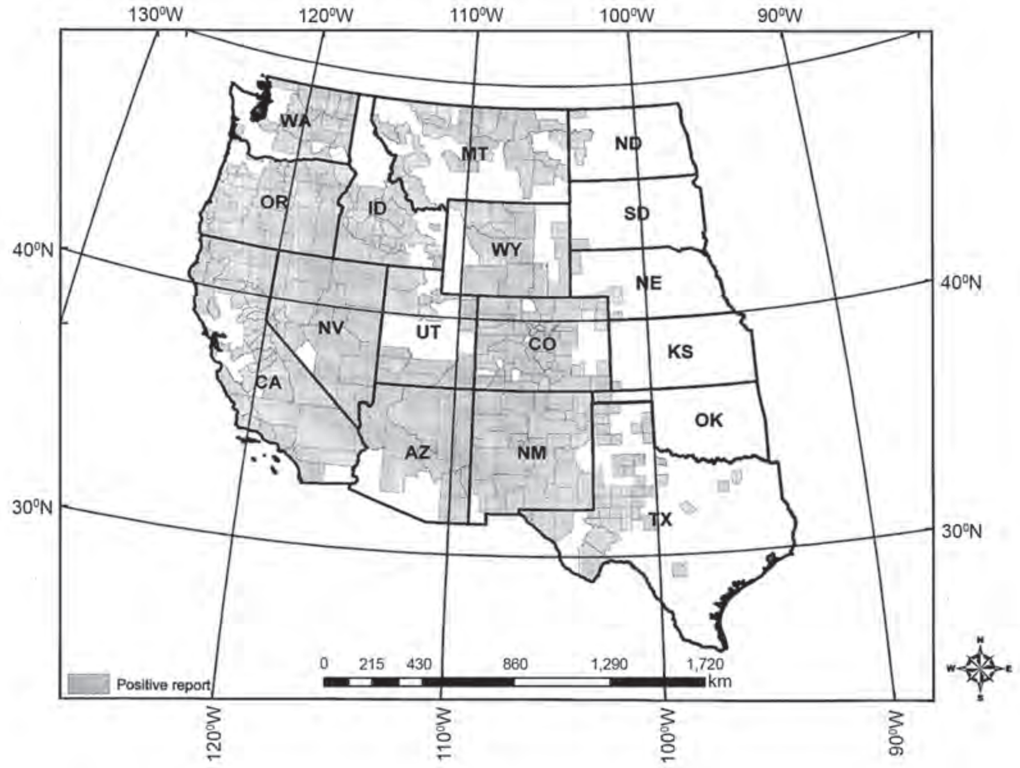


Figure 1. Counties with plague-positive mammals or fleas (1970–present). Figure courtesy of Centers for Disease Control and Prevention.

black-footed ferret (*Mustela nigripes*), are both severely affected by plague, and recovery efforts for black-footed ferrets are hampered not only by the fact that plague outbreaks eliminate the ferrets' prey but also because the ferrets themselves are extremely susceptible to the disease (Williams and others, 1994; Biggins and Kosoy, 2001b; Biggins and Godbey, 2003). The devastating impact of plague on these and other mammalian species of conservation interest has resulted in a renewed emphasis on identifying means for managing plague, including techniques as diverse as insecticidal control of vector fleas and immunization of animals with recombinant vaccines (Creekmore and others, 2002; Seery and others, 2003; Mencher and others, 2004; Rocke and others, 2004). Biggins and Godbey (2003) also discuss partial solutions to the problem of black-footed ferret recovery, including means for increasing breeding in captive populations, increasing survival of released animals, and taking advantage of South Dakota sites that are located slightly east of the known distribution of plague.

In order to more effectively manage and reduce human and wildlife risks associated with plague, we must improve our understanding of the factors that influence transmission, the occurrence and spread of epizootics, and the ability of plague to maintain itself in natural foci. This article provides a brief update on our current knowledge of plague ecology and describes how recent research has contributed to a better understanding of the topic and improved methodologies for studying plague. Also discussed are the many gaps in our knowledge of how plague is maintained in natural foci, what roles certain rodent and vector species play in transmission dynamics, and how environmental factors influence the occurrence, spread, and persistence of epizootics.

The Plague Bacterium and Its Origins

Yersinia pestis is a gram-negative bacterium belonging to the family Enterobacteriaceae. Unlike other members of this group, which are transmitted through fecal-contaminated food and water and live in the guts of their hosts, *Y. pestis* is typically spread from host to host through the bites of infectious fleas and inhabits the blood, as well as lymphatic and reticuloendothelial systems, of its hosts. This dramatic shift in mode of transmission and vertebrate host habitat appears to have been associated, at least in part, with the acquisition of genes that encode virulence and transmission factors. Homologous genes for some *Y. pestis* virulence factors can be found in other species of *Yersinia*, including *Y. pseudotuberculosis*. The origin of genes encoding other virulence or transmission factors is not always clear, but most evidence suggests they were acquired through horizontal transfer of genetic material from other enteric bacteria (Prentice and others, 2001; Gage and Kosoy, 2005). The virulence factors of *Y. pestis* play important roles in enabling host invasion, dispersal within the host, or development of high level bacteremias that greatly increase the likelihood that blood-feeding fleas will imbibe sufficient *Y. pestis* to become infected and later transmit the plague bacterium to other hosts. *Yersinia pestis* transmission factors promote survival of the plague bacterium in the guts of vector fleas and its transmission by these insects. For a more thorough review of virulence and transmission factors and their role in maintaining the natural transmission cycle of plague, see reviews by Perry and Fetherston (1997), Hinnebusch (2003), and Gage and Kosoy (2005).

Until relatively recently, it was believed that the plague bacterium first appeared many millions of years ago, perhaps as early as the upper Oligocene or lower Miocene (Kucheruk, 1965). According to Kucheruk (1965), plague initially arose in cricetid rodents living in semidesert and desert environments. He based these conclusions on an analysis that indicated that the predominant plague hosts in Asia, Africa, and the Americas belonged to the Cricetidae, a family that at the time of Kucheruk's publication included gerbillines, cricetines, arvicolines, and sigmodontines. While this suggestion is still generally accepted, other former Soviet researchers have recently proposed that *Y. pestis* first evolved in marmots (*Marmota* spp.) and their fleas (Suntsov and Suntsova, 2000).

Recent molecular studies clearly indicate that *Y. pestis* is very closely related to the gut microbe *Y. pseudotuberculosis* (Bercovier and others, 1980; Trebesius and others, 1998). The high degree of relatedness between these two bacteria strongly suggests that they have diverged only recently, as suggested by Achtman and others (1999), who proposed that *Y. pestis* might have arisen as a clone of *Y. pseudotuberculosis* only 1,500–20,000 years ago (Achtman and others, 1999; Wren, 2003). This last finding is particularly interesting because of its implications for the degree of coadaptation or coevolution that might have occurred between *Y. pestis* and its hosts and vectors. The recently reported genomic sequences of three *Y. pestis* strains also reveal many interesting features of this bacterium and support the contention that the *Y. pestis* genome is still in a state of rapid flux and might be undergoing reductive evolution as it loses the ability to express certain genes that remain active in *Y. pseudotuberculosis* but are not required for *Y. pestis* to be maintained in a vector-borne transmission cycle (Wren, 2003). Indeed, it has been suggested that the disruption of genes still expressed in *Y. pseudotuberculosis* might be essential for *Y. pestis* to survive in a vector-vertebrate host life cycle (Wren, 2003).

The actual geographic origin of the plague bacterium was a subject of considerable speculation during much of the 20th century. Based on the analysis of plague hosts cited in the previous paragraph, Kucheruk (1965) felt that *Y. pestis* probably appeared in either North American or Asian cricetids. More recent lines of reasoning, however, suggest that a North American origin is highly unlikely. First, epidemiologic evidence strongly indicates that plague did not exist in the United States prior to the last pandemic when rat-infested ships introduced *Y. pestis* to the San Francisco area around 1900 (Link, 1955; Barnes, 1982). Second, microbiological evidence indicates that North American isolates almost invariably reduce nitrates to nitrites but fail to acidify glycerol, which identifies them as belonging to the orientalis biovar that was involved in the late 19th and early 20th century pandemic mentioned above (Devignat, 1951; Guiyoule and others, 1994). Even more convincing results have been provided by recent molecular investigations, including ribotyping and single nucleotide polymorphism analyses, which indicate that United States strains are genetically similar to other orientalis biovar strains collected from areas in other continents that also experienced rat-associated outbreaks during the last pandemic (Guiyoule and others, 1994; Achtman and others, 2004). In general, most lines of evidence, including levels of strain diversity within particular geographic regions, suggest an Asian origin for *Y. pestis*, although the plague bacterium clearly has existed in Africa for more than a millennium and probably considerably longer.

The availability of appropriate methodologies for detecting and analyzing variations among plague strains will have a significant impact on our ability to understand the evolution of plague and how strain differences influence various aspects of *Y. pestis* biology, including its ecology, virulence, and modes of transmission. Early attempts to analyze variation among plague strains relied primarily on phenotypic characteristics, such as reactivities in various biochemical tests, virulence for different types of laboratory animals, production of selected virulence factors, or apparent host associations (Devignat, 1951; Tumanskii, 1957, 1958; Levi, 1962; Stepanov, 1975; Kozlov, 1979). More recently, investigators have analyzed variation among *Y. pestis* strains by using DNA probes, ribotyping, multiple locus variable number tandem repeat assays (MLVA), and analyses of IS100 elements and single nucleotide polymorphisms (Guiyoule and others, 1994; Gorshkov and others, 2000; Klevytska and others, 2001; Motin and others, 2002; Achtman and others, 2004; Girard and others, 2004). Many of the above studies were intended primarily to demonstrate the feasibility of using a particular system for analyzing variation and, thus, examined mostly strains from established reference collections. By contrast, Girard and others (2004) used MLVA to track the spread of plague during an actual epizootic in prairie dogs in northern Arizona. These authors also used their MLVA results, in conjunction with other field and laboratory data, to construct a mutation-rate model that suggested that plague dynamics in their systems consisted of a rapid expansion phase, which was associated with population growth and dispersal, followed by a persistent phase characterized by lower reproduction and dispersal rates. The identification of additional markers should be favored by the recent publication of the complete genomic sequences of three *Y. pestis* strains (Parkhill and others, 2001; Deng and others, 2002; Song and others, 2004).

The phenotypic and genetic studies cited in the previous paragraph identified differences among strains from different foci and host sources, but they fail to answer the question of whether the observed differences among *Y. pestis* strains simply reflect geographic variation or actually provide evidence that regional variants of *Y. pestis* are indeed adapted to a particular host species. Fortunately, the new molecular methodologies described earlier should provide researchers with valuable tools for answering this question as well as other important ecological and evolutionary questions. Analyses of North American strains should be particularly interesting because, as indicated previously, *Y. pestis* apparently has existed in this continent for only a little over 100 years, and the few orientalis biovar strains that were introduced at that time probably were highly similar, having originated in the same region of southwest China. Because the diversity among these invading strains of *Y. pestis* was very low, researchers have an interesting opportunity to examine how *Y. pestis* changes over time and whether this bacterium is likely to exhibit different characteristics, such as increased or decreased virulence, when it is associated with a particular host or vector species.

Plague Transmission Cycles and Maintenance of Plague in Natural Foci

Figure 2 presents a generalized illustration of the natural transmission cycle of plague. In order for flea-borne transmission of plague bacteria to occur, a flea must take a blood meal from a rodent with a heavy *Y. pestis* bacteremia, become infected with plague bacteria, and later transmit this bacterial infection to another susceptible rodent host. Some researchers assume that rodent-to-flea-to-rodent transmission can occur indefinitely in so-called enzootic cycles that cause few apparent deaths among the purportedly resistant rodent hosts (enzootic or maintenance hosts) of these cycles. According to this same concept of plague maintenance and transmission, the disease occasionally spills over to other much more susceptible hosts (epizootic or amplification hosts) that often die in rapidly spreading epizootics, thereby posing increased plague risks for other mammals, including humans (Poland and Barnes, 1979; Poland and others, 1994). As indicated in fig. 2, *Y. pestis* occasionally is transmitted through consumption of infected prey or, perhaps, as a result of inhaling infectious respiratory droplets from animals with pneumonic plague and cough. The roles of these last two modes of transmission in maintaining natural foci have not been determined but are generally assumed to be less important than flea-borne transmission. A few researchers also have proposed that hosts can acquire plague as a result of digging in soil containing viable *Y. pestis* (Mollaret, 1963). Such infections presumably would be acquired through breaks in the skin or inhalation of *Y. pestis* stirred up by an animal’s digging activities.

Rodent Hosts of Plague

Based on early observations in India and elsewhere (Pollitzer, 1954), plague initially was believed to exist in

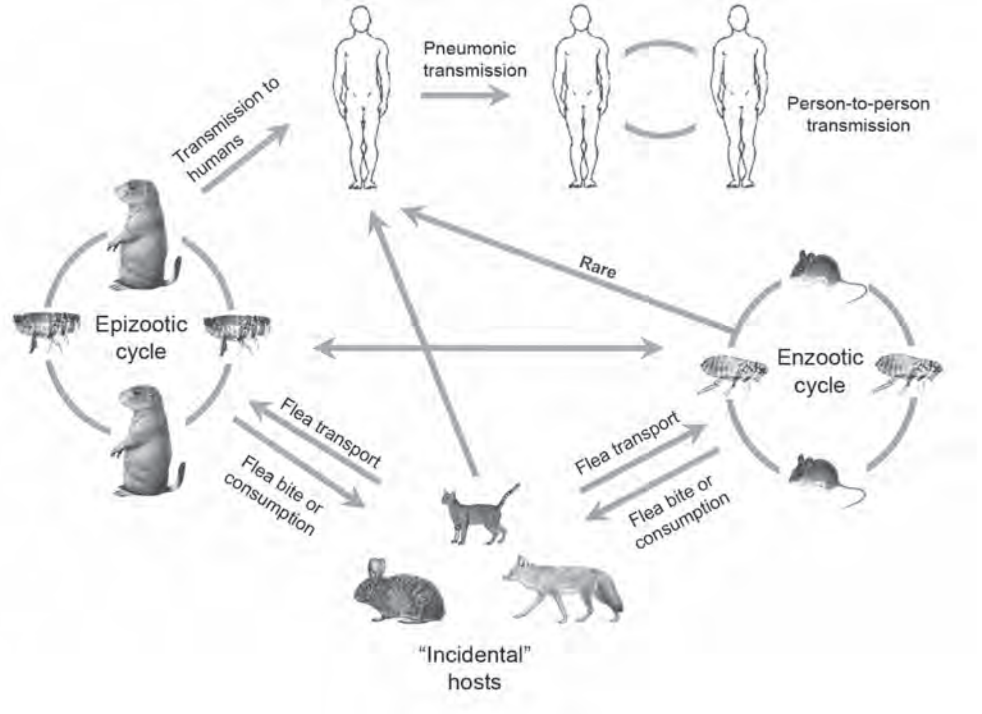


Figure 2. Generalized plague transmission cycle for the United States. Figure courtesy of Centers for Disease Control and Prevention.

nature almost exclusively in commensal rats (primarily *Rattus rattus* and *R. norvegicus*) and rat fleas (primarily *Xenopsylla cheopis*), but it soon became clear that *Y. pestis* also could be found in a variety of wild (noncommensal) rodents and their fleas. In the first decade of the 20th century, McCoy (1908) reported plague among California ground squirrels (*Spermophilus beecheyi*), and others noted soon thereafter that although epizootic activity among rats had largely disappeared, the disease continued to persist in other small mammals around the San Francisco Bay area (Link, 1955). In Asia, Zabolotny (1915) suggested the possibility of wild rodent foci, noting that pneumonic plague outbreaks in Manchuria probably originated from hunters handling tarbagans (*Marmota sibirica*) rather than as a result of human exposure to infectious rat fleas. Later studies confirmed that *Y. pestis* could persist among a variety of rodent species and their fleas without the involvement of commensal rats (Pollitzer, 1954; Pollitzer and Meyer, 1961).

Following the recognition that certain wild rodents are the major hosts of plague, researchers began to ask what characteristics allow particular rodent species to play important roles in the ecology of plague while others play little or no role. At first glance the number of potential rodent hosts is surprisingly high. Pollitzer (1960) identified 203 rodent species or subspecies reported to be naturally infected with *Y. pestis*, a list that could now be slightly extended. However, only a few of these species can be considered truly important hosts of plague, primarily those belonging to the families Sciuridae and Muridae. Among the sciurids, the predominant plague hosts include members of certain genera of burrow-dwelling squirrels (*Spermophilus* [formerly *Citellus*], *Cynomys*, *Ammospermophilus*) and chipmunks (*Tamias*, including *Eutamias* and *Neotamias*). Within the Muridae a number of species in the subfamilies Murinae, Gerbillinae, Arvicolinae, and Sigmodontinae are considered to be important hosts in various regions (Kucheruk, 1965; Gage, 1998; Gratz, 1999).

Among the topics discussed in this paper, probably the most neglected by recent researchers has been the response of native rodent species to *Y. pestis* infection and the roles these animals play in the long-term maintenance of plague foci in different regions. Although many rodents are mentioned in the literature as major plague hosts, the actual evidence to support these claims is often weak, particularly for those putative host species found in certain regions where relatively little research has been done (Gage, 1998; Gratz, 1999). Factors believed to influence the suitability of a particular rodent host for plague include the degree of its population-level resistance to *Y. pestis*-related mortality, its ability to serve as a source of infection for suitable flea vectors, the presence of large numbers of fleas on many members of the host population throughout much of the year, and occupation of burrows or nests that support development and maintenance of high flea populations (Pollitzer and Meyer, 1961; Gage and Kosoy, 2005).

Among these factors, one of the most contentious has been the degree to which population-level resistance to *Y. pestis*-related mortality is essential for the maintenance of plague by one or more rodent species in a particular focus (Pollitzer and Meyer, 1961; Gage and Kosoy, 2005). Host resistance to plague is undoubtedly influenced by many factors, including species, genetic factors within and among populations of a particular species, age, breeding status, prior immunity, physiologic condition, and probably other considerations. When assessing the importance of resistance, it is clear that its presence could favor the survival of host populations in plague-affected areas, although other factors also could operate to reduce mortality and prevent total die-offs among these animals, including the presence of patchy environments that could provide refuges for subpopulations within a larger metapopulation. Seasonal changes in the activities of susceptible hosts or competent flea vectors also might temporarily interrupt or slow down transmission to the point where host populations could be sustained from year to year by recruitment of new individuals (Pollitzer and Meyer, 1961).

One problem encountered in discussing resistance among plague hosts is the somewhat confusing use of the term itself. Host populations that are considered resistant rarely, if ever, are uniformly resistant to *Y. pestis*-related mortality but typically consist of a mixture of somewhat resistant individuals that become infected but recover and other animals that are more susceptible and succumb to plague. For example, mortality rates among great gerbils (*Rhombomys opimus*), which are considered resistant hosts, typically are 40–60 percent (Petrunina, 1951; Rivkus and others, 1973). Although this figure appears high, it is significantly lower than the mortality rates experienced by many other rodents, including other sympatric species of gerbils in the genus *Meriones*. Others have demonstrated that resistance can be associated with past exposure to plague (Birukova, 1960; Thomas and others, 1988; Levi, 1994). Several experiments demonstrated differences in plague resistance between populations of midday gerbils (*Meriones meridianus*) from different sides of the Volga River (Birukova, 1960; Levi, 1994). Levi (1994) compared median lethal doses (LD50) of *Y. pestis* for live-caught gerbils from a population on the west side of the river and another from the east side and found that in three trials, the LD50 values for populations on the west side were 2, 4, and 216 colony forming units (CFUs) while those on the east side of the Volga exhibited LD50 values of 3.397×10^6, 1.000×10^6, and 39.400×10^6 CFUs. Captive-born hybrids of representative individuals (F1 generation) from both populations exhibited intermediate levels of resistance, as did the offspring of these individuals (F2 generation), suggesting that the observed resistance had a genetic basis. According to Levi (1994), these experiments helped explain how midday gerbils are able to serve as primary hosts for plague on the east side of the Volga but have a lesser role west of the river. Interestingly, these same populations of midday gerbils did not differ in their sensitivities to infection with the agents of tularemia and brucellosis. These authors also noted that two populations of another gerbil species, the tamarisk gerbil (*Meriones tamariscinus)*, from the western and eastern sides of the Volga were found to be highly sensitive to plague infection (LD50 values of 6.800 x 10^2 and 5.000 x 10^2 CFUs, respectively).

In North America, Thomas and others (1988) demonstrated that captive-born northern grasshopper mice (*Onychomys leucogaster*) from a plague-free region of Oklahoma were much less resistant to plague than were mice of the same species from a north-central Colorado population that had been exposed to plague. In another North American paper, Quan and Kartman (1956) demonstrated that different populations of deer mice (*Peromyscus maniculatus*) and California voles (*Microtus californicus*) varied in their susceptibility to *Y. pestis*. Differences in susceptibility have been demonstrated to have a genetic basis in California voles (Hubbert and Goldenberg, 1970). Although the above data indicate that populations of some rodent species are highly resistant to *Y. pestis*, others, such as those of the black-tailed prairie dog, nearly always succumb to infection whenever they are struck by plague epizootics (Poland and Barnes, 1979; Biggins and Kosoy, 2001a,b).

Regardless of whether resistant hosts must be present in order for plague foci to persist, flea-borne transmission of plague bacteria among rodents depends on the presence of animals that are capable of serving as sources of infection for feeding fleas. Experimental results indicate that fleas are likely to become infected with *Y. pestis* only after feeding on animals that have very high bacteremias ($>10^6$ *Y. pestis*/mL blood) (Burroughs, 1947; Engelthaler and others, 2000). In general, animals that have such high bacteremias often appear moribund, and few, if any, survive their infections. Thus, resistant animals that develop little or no bacteremia following infection probably are unlikely to serve as significant hosts for infecting fleas. Resistant individuals that survive infection could, however, still play important ecological roles by serving as hosts for maintaining flea populations and contributing offspring to the next generation of hosts. While many of the offspring of these animals also might be resistant, it is possible that at least some of their littermates will be susceptible.

Some animals might not be completely resistant, at least in the sense of being able to rapidly clear themselves of infection, but rather survive their initial bout of illness and go on to develop a chronic infection with *Y. pestis*. While evidence for chronic infections among North American species is almost nonexistent, the phenomenon has been observed in laboratory rats infected with nonencapsulated plague (F1-minus) strains (Williams and others, 1975; Williams and Cavanaugh, 1983). If wild rodents were chronically infected with fully virulent *Y. pestis* and later experienced a recrudescence of infection, perhaps as a result of breeding stress or decreased immune function in older individuals, they could develop a fatal bacteremia of sufficient magnitude to infect feeding fleas.

As noted above, differences of opinion exist about the importance of resistance among host populations. Some researchers have suggested that the role a particular host population plays in plague maintenance can be inferred largely from its level of resistance (Pollitzer, 1954; Pollitzer and Meyer, 1961; Rall, 1965). For example, great gerbils are believed to be the major hosts of plague in certain central Asian desert foci. The percentage of resistant animals among great gerbil populations in these foci has been reported to be 40–60 percent, a level that is higher than that found in gerbils of the genus *Meriones*, which occur in the same foci (Rivkus and others, 1973). In other situations resistance does not appear to differ greatly among various potential host species, making it difficult to assert that one host is more important than another based strictly on the observed levels of host resistance. For example, resistance was similar among great gerbils (50–80 percent), little susliks (*Spermophilus pygmaeus*) (50–70 percent), and midday gerbils (44–60 percent) in a Kazakh steppe focus (Atshabar, 1999).

Others have argued that the importance of resistance can be overemphasized and that other mechanisms can lead to the persistence of plague among highly susceptible host species (Pollitzer, 1954). While plague might kill most animals in a highly susceptible population, survival can be influenced by age, season, or physical condition, thus allowing some hosts to survive and reproduce. Rodents also might be able to become infected shortly before entering hibernation, develop a latent infection as their body temperatures drop, and then not experience severe illness or die of plague until they reawaken in the spring (Gayskii, 1944; Pollitzer, 1954; Pollitzer and Meyer, 1961). Maevskii and others (1999) also reported that *Y. pestis* could be isolated from the “mummified” carcasses of long-tailed susliks (*S. undulatus*) for 7.5 months after these animals first entered hibernation. Spatial isolation among colonies or subpopulations of highly susceptible hosts also could allow plague to be maintained in metapopulations of these animals (Pollitzer and Meyer, 1961; Gage and Kosoy, 2005). In those foci where highly susceptible hosts live in a mosaic of distinct habitat patches, plague is unlikely to kill all of the susceptible animals in each patch or go from patch to patch without at least some delay, thereby allowing the disease to persist by spreading from patch to patch at a rate that is low enough to allow host populations in previously affected patches to recover before once again being exposed to *Y. pestis* infection.

Types of Plague Hosts

Another unresolved question about the role of different rodent hosts in the natural cycle of plague is whether a single host or multiple hosts are required for long-term maintenance of natural transmission cycles. Fenyuk (1940, 1948) believed that certain rodent species and their fleas could maintain plague in the absence of other rodent species and referred to such animals as primary hosts. Secondary hosts were those species that routinely become infected but are incapable of supporting long-term maintenance of *Y. pestis* in a particular focus. Although secondary hosts are by definition incapable of maintaining plague foci in the absence of primary hosts, some proponents of this concept believe they are important in spreading the disease during epizootics.

Expanding on the primary host hypothesis, Rall (1965) proposed the concept of monohostality wherein maintenance of plague in a particular focus depends on the presence of a single rodent species and its fleas. Probably the most commonly cited examples of monohostal foci are those involving great gerbils in central Asia (Petrov, 1959). Acceptance of this proposal has not been universal, and maintenance of plague in other Asian foci has been suggested by other investigators to involve multiple host species (polyhostal foci) (Kalabukhov, 1965). The "Daurian enzootic area" of central Asia represents a proposed polyhostal focus, with Siberian marmots (*M. sibirica*), Daurian susliks (*S. dauricus*), pikas (*Ochotona* spp.), and voles (*Microtus* spp.) all presumedly playing important roles in maintaining this plague focus (Kalabukhov, 1965). The question of whether various United States foci are monohostal or polyhostal has received little attention. Although existing evidence does not allow firm conclusions to be made, *Y. pestis* infections are frequently identified in multiple rodent species in the western United States, particularly in certain southwestern States (New Mexico, Colorado, Arizona) and some mountainous regions of California and nearby areas (Barnes, 1982; Gage and others, 1995), suggesting that at least some of these foci are polyhostal.

American workers have rarely used the terms primary and secondary hosts or monohostality and polyhostality. Instead, the most commonly cited concept categorizes rodent hosts as either enzootic or epizootic (Poland and Barnes, 1979; Poland and others, 1994). Supporters of this concept suggest that enzootic hosts and their fleas maintain plague during interepizootic periods and share certain features, including heterogeneous population responses to *Y. pestis* infection, low mortality following infection, long multiestrous breeding seasons with high reproductive potential, short life expectancies, flea infestations during all seasons, and a relatively high likelihood that antibody will be detected within the population. The most commonly proposed enzootic hosts are various species of *Peromyscus* and *Microtus*. By contrast, epizootic hosts are considered to have low to moderate resistance to *Y. pestis* infection, often experience high morbidity and mortality when infected, exhibit relatively little population-level heterogeneity to infection, and often experience heavy infestations with one or more species of vector flea that are likely to peak in abundance during the warmer months of the year, which is the time when transmission rates also appear to be highest. Proposed epizootic hosts include various species of *Cynomys*, *Spermophilus*, *Ammospermophilus*, *Tamias*, and *Neotoma* (Barnes, 1982; Gage and others, 1995).

In reality, evidence to support the enzootic-epizootic host concept is often lacking or questionable. Obviously, epizootics with dramatic die-offs do occur among proposed epizootic hosts, but corresponding data to indicate that supposed enzootic hosts, such as deer mice or voles, are essential for the maintenance of plague during interepizootic periods is largely lacking. Another plausible alternative is that plague does not rely on any one host for its maintenance in a particular focus during the intervals between epizootics, but rather circulates at much reduced rates among most, if not all, of the same hosts that commonly become infected during epizootics. Under such circumstances, a fair amount of mortality could occur among these hosts during interepizootic periods but go virtually undetected because of the lack of routine rodent surveillance in most plague-enzootic areas.

The Role of Fleas in Transmitting *Yersinia pestis*

Because of its obvious role in rat-associated bubonic plague outbreaks during the last pandemic, many early studies concentrated on the role of the Oriental rat flea (*Xenopsylla cheopis*) as a vector of plague. Within two decades after Yersin's 1894 discovery of the plague bacterium, Bacot and Martin (1914) demonstrated that *Y. pestis* proliferates in the midgut and proventriculus of an infected flea, forming recognizable colonies within a few days after the fleas ingest an infectious blood meal. They also showed that *Y. pestis* colonies can proliferate in an infected flea to such an extent that its proventriculus, a globular spine-filled structure at the end of the foregut, becomes blocked by a mass of bacteria and blood cell remnants. Once blockage of the proventriculus occurs, blood is no longer able to pass through the foregut to the midgut or "stomach" of the flea, resulting in its eventual starvation. Because the blocked rat flea is starving, it will repeatedly attempt to feed on almost any available mammalian host, including humans. As the flea repeatedly fails in its efforts to ingest blood, it attempts to clear the proventricular blockage by regurgitating, a process that does not clear the block but can dislodge plague bacteria from it. These dislodged bacteria and a small amount of ingested blood are then flushed back into the bite wound, resulting in infection of the host. Fleas that fail to become blocked were found to transmit at much lower rates or not at all, which led to the currently accepted dogma that the only efficient plague vectors are those that become blocked.

Within the past decade the molecular basis by which *Y. pestis* promotes blocking in infected *X. cheopis* has become clear (Hinnebusch, 1997, 2005). Hinnebusch and others (1996) demonstrated that *Y. pestis* strains containing mutations in certain genes (hmsR and hmsH) found in the hemin storage (hms) locus were incapable of forming blockages in infected *X. cheopis* fleas. The hemin storage locus derives its name from the ability of strains that possess a functional hms locus to bind hemin to their surfaces. In general, hemin-binding strains appear to be more "sticky" than strains that cannot bind hemin and are, thus, more likely to form clumps of *Y. pestis* in the flea's gut or adhere to the cuticular spines in its proventriculus (Bibikova, 1977; Hinnebusch and others, 1996). Other investigators have demonstrated that blocking depends on temperature, with fleas rarely becoming blocked, or actually clearing themselves of blockages, when maintained at temperatures above 27.5°C (Cavanaugh, 1971; Hinnebusch and others, 1998).

Additional studies have demonstrated that survival of plague bacteria in flea midguts depends on the expression of a gene (ymt) found on the largest of the three *Y. pestis* plasmids (approximately 110 kb) (Hinnebusch and others, 2002). The product of this gene (Ymt), which is a phospholipase D, has been referred to as murine toxin because of its high toxicity for murines (rats and mice) but not other types of rodents or mammals belonging to other orders. The study by Hinnebusch and others (2002), however, suggests that the true function of Ymt is to promote the survival of *Y. pestis* in the flea vector and that its toxicity for murines is merely coincidental. Even more recent studies have suggested that colonization of flea guts by *Y. pestis* might depend on biofilm formation by the plague bacterium (Darby and others, 2002; Jarrett and others, 2004).

This research has greatly improved our understanding of how *Y. pestis* promotes its transmission by flea vectors, but we still have little knowledge of why some flea species, including those found on wild rodents and presumed to be important vectors, vary so greatly in their ability to transmit plague (Gage and Kosoy, 2005). Taxonomic affinities appear to provide little guidance, as demonstrated by the pulicid fleas of the genus *Xenopsylla*. The Oriental rat flea (*X. cheopis*) and a less widely distributed African rat flea (*X. brasiliensis*) are both highly efficient vectors, but their congener *X. astia*, which is common on rats in the Indian subcontinent and southeastern Asia, is a very poor vector (Pollitzer, 1954). Many decades ago, it was hypothesized that the structure or arrangement of the proventricular spines might be important determinants of a flea's ability to transmit *Y. pestis* (Eskey and Haas, 1940). In support of this contention, Korzun and Nikitin (1997) reported that blocking in a ground squirrel flea, *Citellophilus tesquorum*, was positively associated with high levels of fluctuating asymmetry among the proventricular spines of these fleas.

Although the structure of the proventricular spines might very well influence the blocking process, it does not explain why *Y. pestis* appears to be unable to survive and develop in the guts of certain fleas. Among the poorest plague vectors are a number of flea species commonly associated with man and his domestic animals, including the so-called human flea (*Pulex irritans*), the cat flea (*Ctenocephalides felis*), the dog flea (*C. canis*), and sticktight fleas (*Echidnophaga gallinacea*) (Pollitzer, 1954). For example, *P. irritans* often clear themselves of infection within days after ingesting an infectious blood meal and rarely become blocked. Although these insects can transmit plague, they appear to do so only when large numbers of fleas are placed on susceptible hosts within a few hours after being allowed to feed on a *Y. pestis*-infected animal, suggesting that hosts are infected through the introduction of plague bacteria on contaminated flea mouthparts (mechanical transmission) rather than by the feeding of blocked fleas (Pollitzer, 1954; Blanc, 1956). It should be noted that despite its poor vector competency, some authorities believe that *P. irritans* is a significant vector of plague to humans in those situations where people live in unsanitary, heavily flea-infested homes that are often shared with domestic animals (Pollitzer, 1954; Blanc, 1956). These findings raise the possibility that infected but unblocked fleas on wild rodents also might transmit plague bacteria under certain circumstances.

Fleas found on wild rodent hosts also vary considerably in their ability to support *Y. pestis* infections and transmit plague bacteria (Eskey and Haas, 1940; Douglas and Wheeler, 1943; Burroughs, 1944, 1947; Holdenried, 1952; Pollitzer, 1954; Kartman and Prince, 1956; Kartman, 1957; Kartman and others, 1958a,b; Pollitzer, 1960; Pollitzer and Meyer, 1961; Engelthaler and others, 2000). While some wild rodent fleas appear to block at high rates and become infectious soon after ingesting a *Y. pestis*-containing blood meal, other species require considerably longer periods of time to become blocked. The time required for blocking to occur in some species is sufficiently long that most of the infected fleas are likely to die before block formation actually occurs. A recent comparison of the development of *Y. pestis* infections in *X. cheopis* and *Oropsylla montana*, a ground squirrel flea, demonstrated that *Y. pestis* colonies became established very early in the course of infection in both the proventriculus and the midgut of infected *X. cheopis* (Engelthaler and others, 2000). In *O. montana*, however, *Y. pestis* colonies initially appeared only in the midguts of infected fleas, which meant that the midgut infection had to proliferate and spread considerably before colonization of the proventriculus could occur. Because colonization of the proventriculus is delayed, the average time required for blocking to occur in *O. montana* is much longer than in *X. cheopis*. The failure of many *O. montana* to become blocked and the fact that these fleas transmit at much lower rates than *X. cheopis* are particularly interesting because *O. montana* is considered to be the primary vector of plague to humans in the United States. Published results of experimental infection and transmission studies (see citations at the beginning of this paragraph) done with other species of wild rodent fleas suggest that the situation observed for *O. montana* is more typical than that seen with *X. cheopis*. Of particular interest are the limited studies done with ground squirrel, prairie dog, and woodrat (*Neotoma* spp.) fleas, which typically indicate that most of these fleas are relatively poor plague vectors compared to *X. cheopis* (see earlier citations in this paragraph). While many wild rodent fleas reportedly block and transmit at low rates, a few, such as *Hystrichopsylla dippei*, appear to be quite efficient vectors (Kartman and others, 1958b). Although the studies cited earlier in this paragraph make it obvious that *X. cheopis* is an exceptional plague vector, this does not mean that *Y. pestis* is always successful in its attempts to colonize and establish a stable infection in this flea. Engelthaler and others (2000) found that by 6 weeks after ingesting a *Y. pestis*-infected blood meal, 60 percent of all *X. cheopis* had cleared themselves of infection. Despite this fact, however, the infection rates observed in *X. cheopis*

6 weeks after taking an infectious blood meal were still much higher than those observed in *O. montana* (60 percent versus 15 percent, respectively).

Many of these studies raise questions about whether transmission by blocked fleas is actually essential for the rapid spread of *Y. pestis* during epizootics or for the interepizootic maintenance of plague. One possibility is that in some situations partially blocked fleas could transmit at sufficiently high rates to be important vectors. Burroughs (1947) and Engelthaler and others (2000) demonstrated that *O. montana* fleas were capable of transmitting within 4 days after feeding on an infectious host, a much shorter time than that required for blockage in these species, but perhaps too long for strictly mechanical transmission of viable *Y. pestis* on contaminated mouthparts to occur. Burroughs (1947) and others (Voronova, 1989; Degtyareva and others, 1990; Gan and others, 1990; Bazanova and others, 1991) list additional examples of the transmission of *Y. pestis* by partially blocked or apparently block-free fleas.

The role that mechanical transmission might play in natural foci also should be reexamined. As noted previously, early studies of potential plague vectors indicated that some fleas, such as the human flea, rarely became blocked but occasionally transmitted plague when fleas that had fed on an infected host were quickly transferred in large numbers to susceptible hosts, a finding that is typically interpreted as evidence for mechanical transmission (Pollitzer, 1954; Blanc, 1956). Later studies, particularly those of Burroughs (1944, 1947) and Kartman and others (1958a,b) also provided evidence that common North American rodent fleas are capable of transmitting *Y. pestis* by mechanical means. Quan and others (1953) provided interesting evidence that even *X. cheopis* is capable of mechanically transmitting plague bacteria. Based on the results of the studies noted earlier and others, Burroughs (1947) and Kartman and others (1958a,b) suggested that mechanical transmission might be important, particularly during epizootics when host densities are high and the likelihood that fleas will rapidly transfer from dead hosts to susceptible ones is also high. Kartman and others (1958a,b) further suggested that the bulk of transmission during epizootics occurs through mechanical means while transmission of plague during interepizootic periods is accomplished by those rodent fleas that are capable of becoming blocked and transmitting at high efficiencies. In particular, he cited *Malaraeus telchinum*, a flea that is extremely abundant on mice and voles in some regions of the West, as a likely mechanical vector during epizootics and *Hystrichopsylla dippei*, a far less abundant but much more efficient plague vector, as an important vector during interepizootic periods. Unfortunately, others have not pursued this hypothesis, and it would be very interesting to know whether other “pairs” or groups of fleas play similarly complimentary roles during epizootic and interepizootic periods. It also would be worthwhile to determine whether the rapid rates of transmission observed during plague epizootics in prairie dogs or other highly susceptible hosts are due to mechanical transmission or transmission by blocked fleas. The former can take place virtually immediately after a flea has fed on a heavily bacteremic host, but the latter typically requires an extrinsic incubation period of 2 or more weeks before fleas can become blocked and, therefore, capable of efficiently transmitting. Alternatively, hosts might become infected by consuming other animals that have died of plague or through respiratory contact with hosts that have pneumonic plague.

Although laboratory experiments can help determine whether a particular flea species is likely to be an important vector, other factors also need to be considered in determining the actual role a potential vector will play in nature (Gage, 1998; Gage and Kosoy, 2005). Obviously, fleas that feed on hosts that are seldom infected with plague, or live only in plague-free areas, are unlikely to be important. Fleas that are highly host-specific might be very important for transmitting plague among members of a particular host species but would rarely spread the disease to other hosts. The seasonality and abundance of the flea’s hematophagous adult stage also are likely to be important. Many important vectors occur most abundantly on their hosts during those warm months when plague transmission also peaks. Another potentially important factor is the ability of fleas to survive in off-host environments while waiting for an alternative host to appear.

Maintenance of Plague Between Transmission Seasons and Between Epizootics

Figure 2 provides a basic overview of the plague transmission cycle but unfortunately conveys almost no information on the relative roles different components play in maintaining plague between transmission seasons or during interepizootic periods when little or no *Y. pestis*-related illness is apparent among the normal hosts of the disease. At least four different hypotheses can be advanced for long-term maintenance of plague (Gage and Kosoy, 2005): continuous enzootic transmission among rodent hosts and their fleas at more or less steady rates except during irregularly occurring epizootics; chronic infection of rodents with eventual relapses of the disease in these animals and subsequent infection of vector fleas following these relapses; prolonged survival of infected fleas in host nests or burrows; and indefinite survival of *Y. pestis* in soil, soil protozoa, or perhaps even plant tissues. The following sections discuss the above hypotheses of plague maintenance.

Are Rodents Merely Amplifying Hosts or True Reservoirs of Infection?

In order for plague to be maintained through continuous enzootic transmission, the rodent hosts and flea vectors must both be present and active throughout the year. In temperate regions some plague hosts enter hibernation or become much less active during winter months, which could interrupt the *Y. pestis* transmission cycle. For example, marmots (*M. sibirica* and certain other *Marmota* spp.), which are thought to be critically important plague hosts in some Asian foci, hibernate for many months and, thus, are unlikely to become infected after entering hibernation or support ongoing transmission during this period. If their fleas also become inactive during winter months or lack the opportunity to acquire new infections from hibernating hosts, transmission could be interrupted. One possible solution to this dilemma could be the survival of *Y. pestis* in hibernating animals (Gayskii, 1944; Pollitzer, 1954). According to this hypothesis, a *Y. pestis*-infected animal might enter hibernation prior to becoming ill, thus slowing or temporarily halting the progression of *Y. pestis* infection as a result of the effects of low host body temperature on the growth of the pathogen or its virulence. Upon reawakening in the spring, the infection could reactivate, causing the animal to become ill and develop a *Y. pestis* bacteremia of sufficient magnitude to infect feeding fleas, thereby continuing the cycle of rodent-to-flea-to-rodent transmission for another year. While this explanation seems plausible and does have some experimental support, little is known about its importance in natural foci. Also, such an explanation is unlikely to be important in tropical or subtropical foci. If hibernating animals die of plague before reawakening in the spring, it is also possible that plague bacteria could survive in their dried tissues for many months after the animals have died (Maevskii and others, 1999).

According to some investigators, rodents that do not hibernate might develop chronic infections and act as reservoirs for maintaining plague from one transmission season to the next (Pollitzer, 1954; Pollitzer and Meyer, 1961). Experimental evidence suggests that individual great gerbils in central Asia survive infection and then develop granuloma-like lesions in their livers and perhaps other tissues that contain viable *Y. pestis* (Suleimenov, 2004). These plague bacteria-containing lesions can reportedly persist for many months, thereby allowing latent infections to become reactivated during the spring as adult hosts experience increased stress due to breeding or decreased immune system function due to old age. Great gerbils that experience reactivation of their infections are believed to circulate sufficient *Y. pestis* in their bloodstream to infect feeding fleas. One of the practical problems encountered in evaluating the importance of presumed chronic infections in rodents under field conditions is whether lesions observed in the tissues of suspected carrier hosts are really indicative of chronic infection or simply a sign of resolving infections.

Some researchers have argued that plague could be maintained through the winter months by continuous transmission between certain hosts and their fleas. Such a pattern of transmission has been proposed for deer mice (*P. maniculatus*) and their allies (other *Peromyscus* spp.) or various species of voles (*Microtus* spp. and others) (Poland and Barnes, 1979; Poland and others, 1994). Deer mice and other mice of the genus *Peromyscus* remain active in all seasons, are often infested with fleas during the winter months, and reproduce throughout much of the year, which results in the ongoing introduction of susceptible animals into local mouse populations. Whether populations of *Peromyscus* or voles can indeed maintain plague through continuous rodent to flea to rodent transmission is at present uncertain. In a 13-month study (March 1954–April 1955) of 1,458 *Microtus californicus* found dead in a San Mateo County plague focus, *Y. pestis* was identified in the tissues of these animals during 10 of the 13 months. The only months when positive animals were not identified were December 1954 ($n = 52$), March 1955 ($n = 33$) and April 1955 ($n = 27$) (Kartman and others, 1962). Considering the relatively low number of dead animals examined during those 3 months, *Y. pestis* might have indeed been present all year in at least some voles within this focus.

Fleas as Reservoirs of Plague

While no one disputes that fleas are the only significant vectors of plague, they also could act as long-term reservoirs by maintaining *Y. pestis* in off-host environments during the intervals between transmission seasons or during periods of host hibernation (Gage and Kosoy, 2005). Many studies indicate that infected but unblocked, and even blocked, fleas can survive for many months in off-host environments. In one study, infected *Ctenopthalmus breviatus* survived for up to 396 days when held on wet sand at temperatures of 0–15°C (Golov and Ioff, 1926, 1928). Other studies indicated that *Oropsylla silantiewei* could survive for as long as 558 days without feeding while *Citellophilus tesquorum* and *Neopsylla setosa* did so for 275 and 180 days, respectively (cited by Kozlov, 1979). Sharets and others (1958) reported that *Rhadinopsylla ventricosa* fleas remained infected with *Y. pestis* for at least 420 days. Bazanova and Maevskii (1996) succeeded in maintaining more than half of all *C. tesquorum altaicus* fed on infected susliks (*Spermophilus undulatus*) over a period from mid-September to mid-June, which provided sufficient time for these fleas to survive through the hibernation period of their hosts. One female in their experiments survived through two winters, living for a total of 411 days after being fed on an infected suslik. Even more importantly, when infected *C. tesquorum altaicus* that had been starved through the hibernation period of their hosts were later allowed to feed, they succeeded in transferring plague to these animals, thus demonstrating that these fleas could act as both vectors and reservoirs of infection. In North America, Kartman and others (1962) reported the recovery of infected *Oropsylla labis* (syn. *Opisocrostis labis*) and *O. tuberculata cynomuris* (syn. *Opisocrostis tuberculatus cynomuris*) from abandoned prairie dog burrows for more than a year after their hosts had died of plague.

Survival of Plague in Soils, Soil Protozoa, Plant Tissues, or Other Unusual Sites

Some investigators have proposed that plague might survive during interepizootic periods in the soil of burrows (Mollaret, 1963). In one experiment, four species of gerbils (*Meriones libycus*, *M. persicus*, *M. tristrami*, and *M. vinogradovi*) developed plague after being allowed to dig burrows in laboratory enclosures containing soils contaminated on the previous day with *Y. pestis* in a broth culture (Mollaret, 1963). In other experiments, it was claimed that plague survived many months in both sterilized and nonsterilized soils (Mollaret, 1963; Baltazard, 1964). According to supporters of this hypothesis, rodents can become infected by burrowing in soils that are contaminated with the remains or excreta of infected mammals or fleas. Other researchers have expressed skepticism about this hypothesis, noting methodological concerns about the few studies that have been advanced in its support or that the observed patterns of disease spread and host population recovery often fail to agree with the suggestion that new epizootics are initiated through contact of animals with contaminated soils (Gage and Kosoy, 2005). Also, unlike anthrax or certain other soil-dwelling organisms, *Y. pestis* does not form a sporelike structure, and most evidence suggests that plague bacteria die relatively quickly outside their hosts or vectors (Brubaker, 1991; Perry and Fetherston, 1997). Recently, some have presented evidence that plague might be able to survive in soil protozoa rather than in a free state in soils (Nikul'shin and others, 1992; Nersesov and Tsikhistavi, 1997; Domaradsky, 1999; Pushkareva, 2003). Recent studies also have shown that plague bacteria can form biolfilms on a nematode species (*Caenorhabditis elegans*) commonly used in laboratory studies (Darby and others, 2002), but we know of no evidence indicating that soil nematodes become infected under natural conditions. Others have suggested that *Y. pestis* might survive in plant tissues (Rivkus and others, 1993; Litvin, 1997) or in a latent nonculturable state in soils (Suchkov and others, 1997). Although none of these hypotheses has received strong support, they cannot be completely rejected on the basis of currently available data and are worthy of additional research.

Factors Affecting Rates of Plague Transmission and Incidence of Epizootics

One of the most striking aspects of plague is its ability to spread explosively among susceptible animal populations and across landscapes during epizootics. Almost equally striking is the fact that these relatively brief periods of intense transmission are followed by much longer intervals when the lack of obvious mortality among highly susceptible hosts makes it seem as if the disease has completely disappeared from a particular focus. In most instances, however, at least some *Y. pestis* transmission can still be identified in the suspect area through use of a sensitive monitoring technique, such as serosurveys of coyotes or other rodent-consuming carnivores (Gage and others, 1994). While much remains to be learned about the conditions that lead to plague epizootics or halt their progress, transmission rates can be affected by such factors as host resistance, densities of host and vector populations, the length of time that *Y. pestis* can persist in off-host flea populations, the vector competency of local flea species, the length of the extrinsic incubation period before fleas become infective for hosts, the likelihood that rodents will become chronically infected, periods of host inactivity (hibernation or aestivation), and seasonal changes and other climatic factors that influence the timing of host and vector life cycles as well as their survival and reproduction (Pollitzer, 1954; Pollitzer and Meyer, 1961; Poland and Barnes, 1979; Poland and others, 1994; Gage, 1998; Gage and Kosoy, 2005).

One of the most important questions in plague ecology is what conditions lead to the onset of epizootics. Modeling studies of human rat-associated plague suggest that if plague can persist in small rat subpopulations, it will spill over at irregular intervals to other susceptible rat subpopulations, causing epizootics and increased risks of flea-transmitted bubonic plague in humans (Keeling and Gilligan, 2000a,b). In these studies, persistence was favored by a high proportion of resistant individuals, and short-lived epizootics occurred when plague was introduced into subpopulations composed primarily (>80 percent) of susceptible individuals. In a more recent modeling study using rodent plague surveillance data from Kazakhstan, Davis and others (2004) reported that the invasion and persistence of plague in great gerbil populations was related to rodent density. They also found that as populations fell below certain thresholds, plague was likely to disappear from an area that had been invaded earlier in the course of an epizootic.

The suggestion that rodent population densities affect the invasion and persistence of plague in host populations is not surprising but still leaves open the question of what factors initially cause rodent populations in plague foci to increase and epizootic activity to become likely. Human plague risks typically increase greatly during epizootics, and the occurrence of increased numbers of human cases is generally believed to reflect increased epizootic activity. Parmenter and others (1999) analyzed human plague in New Mexico and found that human risks were correlated with increases in cool season precipitation from the previous year. They attributed this increase in human risk to a trophic cascade effect where increased cool season precipitation led to increased food availability for rodents. It was hypothesized that as food availability increases, so do survival and reproduction of rodent hosts and perhaps flea vectors of plague. In agreement with the results of Davis and others (2004), they postulated that increased rodent numbers increase the risk of epizootics, as well as human cases. In a later study, Enscore and others (2002) demonstrated that both late winter precipitation and threshold temperatures were associated with human plague risks in the Four Corners region of the American Southwest. These last authors suggested that the trophic cascade model of Parmenter and others (1999) be modified to include threshold temperature effects that might affect not only rodent populations but also flea survival and reproduction. In particular, they suggested that years with exceptionally high numbers of days above certain threshold temperatures were likely to be those with low flea populations because of the negative effects of hot summer temperatures on flea survival and reproduction, or perhaps the ability of these insects to transmit plague (Cavanaugh, 1971; Cavanaugh and Marshall, 1972; Enscore and others, 2002). Collinge and others (2005b) attempted to test the generality of the trophic cascade model (Parmenter and others, 1999) as modified by Enscore and others (2002) and found that the occurrences of reported plague events in prairie dogs were not associated with certain climatic variables in Boulder County, Colo., but were associated with precipitation and temperature effects in a Phillips County, Mont., site. The authors concluded that the timing and magnitude of precipitation and temperature might influence the occurrence of plague in some but not all areas. They also reported that the best climatic predictors in the Montana site corresponded well with those noted in the above studies of human plague cases in the southwestern United States. In another Colorado study, Stapp and others (2004) demonstrated that epizootics in prairie dogs living on grasslands in north-central Colorado were associated with El Niño events.

Landscape Ecology of Plague

The influence of landscape structure on plague distribution and dynamics has been investigated in only a few of the world's plague foci. Bibikov and others (1963) stated that localities where plague infection can be maintained for a long period of time occupy relatively small portions of the territories that are endemic for plague, and speculated that, for unknown reasons, these sites present more auspicious conditions for the circulation of *Y. pestis* than other sites that are only affected sporadically. In other studies, Alexeev (1991) and Karimova (2002) used landscape characteristics for typing plague foci in desert zones of Kazakhstan and central Asia. Medzykhovsky and others (2001) demonstrated an association between the distribution of plague epizootics in the trans-Uralian steppe regions of eastern Kazakhstan and certain soil and grass characteristics. Serzhanov and others (1982a) found that places where plague persists over long periods of time in central Asian deserts are closely associated with landscapes characterized by abundant underground water lying near the surface (hydrologic lenses). These authors also demonstrated a correlation between the dynamics of plague epizootics and groundwater characteristics in nine different landscapes in Turkmenia. Based on these observations, Serzhanov and others (1982b) proposed the use of hydrothermal indices for the ecological typing of plague foci. In another interesting study, Rotshild (2001) hypothesized that levels of trace metals in natural environments influence the distribution and occurrence of plague. His hypothesis was based on multiple observations in the Altai Mountains, Tuva (eastern Siberia), the Kyzyl Kum desert in Uzbekistan, and a sandy semidesert area of the Caspian lowlands where he found correlations between epizootic plague activity and decreased or increased concentrations of Fe, Co, and Ti and low concentrations of Cu, Ni, and V.

In the United States, plague foci are known to occur in a variety of landscapes in numerous western mountain ranges, the High Plains, and intermountain grasslands (Barnes, 1982). Although plague might make brief epizootic intrusions into some areas, it remains conspicuously absent from certain extremely hot desert regions of the southwestern States, including the Sonoran Desert in southern Arizona. Although the reasons for plague's absence in these areas are unknown, it is tempting to speculate that the extremely hot, dry conditions in these desert areas are likely to limit transmission by fleas because these insects probably face severe desiccation when they are not closely associated with a host or protected burrow system or when they attempt to quest at burrow entrances in such exceptionally hot and dry environments.

A so-called "plague line" appears to exist at about the 100th meridian of longitude, a line that along much of its length marks the zone of transition from the tall grass prairies to the short grass habitats of the High Plains (Barnes, 1982). Among the factors that might influence the location of this "plague line" are rodent and flea diversity and changes in burrow microclimates or other features of burrow ecology. Although some recognized plague hosts occur on the plains, including black-tailed prairie dogs, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), spotted ground squirrels (*S. spilosoma*), and southern plains woodrats (*Neotoma micropus*), the diversity of important plague hosts clearly decreases as one moves away from the Rocky Mountains onto the High Plains. By contrast, numerous rodent hosts of plague occur in relatively close proximity to each other in the lower elevation coniferous woodlands, foothills, and nearby plains. Many of these species, including woodrats, prairie dogs, ground squirrels, and chipmunks, live in burrows or complex nests that are often heavily infested with fleas. Another factor that might be important is the habitat complexity found near the Rockies and on High Plains sites nearest to these mountains. The more varied and patchy habitats around the Rockies could provide partial barriers and slow the movement of plague from one habitat to another, thus providing a limited refuge for some rodent populations and increasing the likelihood that sufficient hosts will survive epizootics and keep transmission going from one season the next. As one moves on to the High Plains, however, the habitats appear to be more homogeneous with fewer barriers to the spread of plague, which could result in rapidly spreading epizootics that kill nearly all susceptible rodents and leave few individuals to support ongoing transmission. Plague probably is unlikely to persist in areas with such relatively homogeneous habitats but could, perhaps, repeatedly invade them when widespread epizootics sweep across the landscape.

Regional or local landscape ecology studies are almost nonexistent in the plague foci of the western United States. A single recent study by Collinge and others (2005a) used logistic regression to analyze two long-term data sets on plague occurrence in prairie dogs. The first of their two study sites was located in Boulder County, Colo., a region subject to rapid human development, and the second was in Phillips County, Mont. Associations were found at both sites between plague occurrence, landscape parameters, and colony characteristics. The best models from both sites predicted positive effects on plague occurrence of proximity to colonies that experienced plague and negative effects of road, stream, and lake cover.

Conclusions

Although some important findings, such as those describing how *Y. pestis* promotes its transmission by flea vectors, have occurred in recent years, many aspects of our understanding of plague ecology have progressed little since the mid-20th century. This is surprising when one considers the exciting new advances in many relevant fields or technologies, including molecular biology, immunology, population genetics, microbiology, geographic information systems, remote sensing, and mathematical modeling. Among the many interesting issues that have yet to be addressed satisfactorily are the degree to which *Y. pestis* exhibits adaptations to major hosts and vectors or vice versa, the relative roles of various factors in determining levels of host resistance, the roles many rodent species play in plague maintenance, the structure of plague foci in North America and elsewhere, the true significance of mechanical transmission or the transmission of plague bacteria by partially blocked fleas, the reasons why different flea species vary so greatly in vector competency, and the roles that climatic variables, landscape features, host and vector densities, or other factors play in influencing the spread of plague or the occurrence of epizootics. Fortunately, many of these questions can now be addressed, as interest in plague and funding for its study have increased as a result of recent concerns about the use of plague as a weapon of bioterrorism and the recognition that *Y. pestis* can adversely impact many wildlife species.

References Cited

Achtman, M., Morelli, G., Zhu, P., Wirth, T., Diehl, I., Kusecek, B., Vogler, A.J., Wagner, D.M., Allender, C.J., Easterday, W.R., Chenal-Francisque, V., Worsham, P., Thomson, N.R., Parkhill, J., Lindler, L.E., Carniel, E., and Keim, P., 2004, Microevolution and history of the plague bacillus, *Yersinia pestis*: Proceedings of the National Academy of Sciences, v. 101, p. 17837–17842.

Achtman, M., Zurth, K., Morelli, G., Torrea, G., Guiyoule, A., and Carniel, E., 1999, *Yersinia pestis*, the cause of plague, is a recently emerged clone of *Yersinia pseudotuberculosis*: Proceedings of the National Academy of Sciences, v. 96, p. 14043–14048.

Alexeev, E.V., 1991, Ecological and geographic characteristics of natural foci of plague: Ekologiya, issue 6, p. 45–51.

Anderson, S.H., and Williams, E.S., 1997, Plague in a complex of white-tailed prairie dogs and associated small mammals in Wyoming: Journal of Wildlife Diseases, v. 33, p. 720–732.

Atshabar, B., 1999, Plague biocenosis as ecological system, *in* Kutirev, V.V., ed., Problemy Osobo-Opasnih Infektsii: Saratov, Slovo Press, v. 79, p. 36–44.

Bacot, A.W., and Martin, C.J., 1914, Observations on the mechanism of the transmission of plague by fleas: Journal of Hygiene (London), v. 13 (Plague suppl. III), p. 423–439.

Baltazard, M., 1964, The conservation of plague in inveterate foci: Journal of Hygiene, Epidemiology, Microbiology, and Immunology, v. 120, p. 409–421.

Barnes, A.M., 1982, Surveillance and control of bubonic plague in the United States: Symposia of the Zoological Society of London, v. 50, p. 237–270.

Bazanova, L.P., and Maevskii, M.P., 1996, The duration of the persistence of plague microbe in the body of flea *Citellophilus tesquorum altaicus*: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 2, p. 45–48.

Bazanova, L.P., Zhovtyi, I.F., Maevskii, M.P., Klimov, V.T., and Popkov, A.F., 1991, The seasonal dynamics of blocking in the flea *Citellophilus tesquorum altaicus* from the Tuva natural plague focus: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 1, p. 24–26.

Bercovier, H., Mollaret, H.H., Alonso, J.M., Brault, J., Fanning, G.R., Steigerwalt, A.G., and Brenner, D.J., 1980, Intra- and interspecies relatedness of *Yersinia pestis* by DNA hybridization and its relationship to *Y. pseudotuberculosis*: Current Microbiology, v. 4, p. 225–229.

Bibikov, D.I., Petrov, V.S., and Khrustselevsky, V.P., 1963, On some ecological and geographical patterns in natural focality of plague: Zoologicheskii Zhurnal (Leningrad), v. 42, p. 1306–1316.

Bibikova, V.A., 1977, Contemporary views on the interrelationships between fleas and the pathogens of human and animal diseases: Annual Review of Entomology, v. 22, p. 23–32.

Biggins, D.E., and Godbey, J.L., 2003, Challenges to reestablishment of free-ranging populations of black-footed ferrets: Comptes Rendus Biologies, v. 326, suppl. 1, p. S104–S111.

Biggins, D.E., and Kosoy, M.Y., 2001a, Influences of introduced plague on North American mammals—implications from ecology of plague in Asia: Journal of Mammalogy, v. 82, p. 906–916.

Biggins, D.E., and Kosoy, M.Y., 2001b, Disruptions of ecosystems in western North America due to invasion by plague: Journal of the Idaho Academy of Science, v. 37, p. 62–65.

Birukova, E.S., 1960, Experimental plague in the tamarisk gerbil *Meriones tamariscinus* and the midday gerbil *M. meridianus* from the eastern Caucasian region, *in* Trudy Protivochumnogo Instituta Kavkaza i Zakavkaz'ya 4: Stavropol', Russia, Stavropol'skoe knizhnoe izdatel'stvo, p. 84–94.

Blanc, G., 1956, Une opinion non conformiste sur la mode de transmission de la peste: Revue d'Hygiene et de Medicine Sociale, v. 4, p. 535–562.

Brubaker, R.R., 1991, Factors promoting acute and chronic diseases caused by yersiniae: Clinical Microbiology Reviews, v. 4, p. 309–324.

Burroughs, A.L., 1944, The flea *Malaraeus telchinum*, a vector of *P. pestis*: Proceedings of the Society for Experimental Biology and Medicine, v. 55, p. 10–11.

Burroughs, A.L., 1947, Sylvatic plague studies. The vector efficiency of nine species of fleas compared with *Xenopsylla cheopis*: Journal of Hygiene, v. 43, p. 371–396.

Cavanaugh, D.C., 1971, Specific effect of temperature upon transmission of the plague bacillus by the Oriental rat flea, *Xenopsylla cheopis*: American Journal of Tropical Medicine and Hygiene, v. 20, p. 264–273.

Cavanaugh, D.C., and Marshall, J.D., Jr., 1972, The influence of climate on the seasonal prevalence of plague in the Republic of Vietnam: Journal of Wildlife Diseases, v. 8, p. 85–94.

Collinge, S.K., Johnson, W.C., Ray, C., Matchett, R., Grensten, J., Cully, J.F., Jr., Gage, K.L., Kosoy, M.Y., Loye, J.E., and Martin, A.P., 2005a, Landscape structure and plague occurrence in black-tailed prairie dogs: Landscape Ecology, v. 20, p. 941–955.

Collinge, S.K., Johnson, W.C., Ray, C., Matchett, R., Grentsen, J., Cully, J.F., Jr., Gage, K.L., Kosoy, M.Y., Loye, J.E., and Martin, A.P., 2005b, Testing the generality of a trophic-cascade model for plague: EcoHealth, v. 2, p. 1–11.

Creekmore, T.E., Rocke, T.E., and Hurley, J., 2002, A baiting system for delivery of an oral plague vaccine to black-tailed prairie dogs: Journal of Wildlife Diseases, v. 38, p. 32–39.

Cully, J.F., Jr., 1997, Growth and life-history changes in Gunnison's prairie dogs after a plague epizootic: Journal of Mammalogy, v. 78, p. 146–157.

Cully, J.F., Jr., Barnes, A.M., Quan, T.J., and Maupin, G., 1997, Dynamics of plague in a Gunnison's prairie dog colony complex from New Mexico: Journal of Wildlife Diseases, v. 33, p. 706–719.

Cully, J.F., Jr., Carter, L.G., and Gage, K.L., 2000, New records of sylvatic plague in Kansas: Journal of Wildlife Diseases, v. 36, p. 389–392.

Darby, C., Hsu, J.W., Ghori, N., and Falkow, S., 2002, Plague bacteria biofilm blocks food intake: Nature, v. 417, p. 243–244.

Davis, S., Begon, M., De Bruyn, L., Ageyev, V.S., Klassovskiy, N.L., Pole, S.B., Viljugrein, H., Stenseth, N.C., and Leirs, H., 2004, Predictive thresholds for plague in Kazakhstan: Science, v. 304, p. 736–738.

Degtyareva, L.V., Labunets, N.F., Osipova, S.P., and Shchedrin, V.I., 1990, The ability of flea species on common vole from mountainous Dagestan to transmit and preserve the causative agent of plague: Parazitologiya, v. 24, p. 106–112.

Deng, W., Burland, V., Plunkett, G., III, Boutin, A., Mayhew, G.F., Liss, P., Perna, N.T., Rose, D.J., Mau, B., Zhou, S., Schwartz, D.C., Fetherston, J.D., Lindler, L.E., Brubaker, R.R., Plano, G.V., Straley, S.C., McDonough, K.A., Nilles, M.L., Matson, J.S., Blattner, F.R., and Perry, R.D., 2002, Genome sequence of *Yersinia pestis* KIM: Journal of Bacteriology, v. 184, p. 4601–4611.

Devignat, R., 1951, Variétés de l'espèce *Pasteurella pestis*—nouvelle hypothèse: Bulletin of the World Health Organization, v. 4, p. 247–263.

Domaradsky, I.V., 1999, Is not plague a "protonosis"?: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 2, p. 10–13.

Douglas, J.R., and Wheeler, C.M., 1943, Sylvatic plague studies. II. The fate of *Pasteurella pestis* in the flea: Journal of Infectious Diseases, v. 72, p. 18–30.

Elton, C.S., 1958, The ecology of invasions by animals and plants: London, Methuen and Co., 181 p.

Engelthaler, D.M., Hinnebusch, B.J., Rittner, C.M., and Gage, K.L., 2000, Quantitative competitive PCR as a method for exploring flea-*Yersinia pestis* dynamics: American Journal of Tropical Medicine and Hygiene, v. 62, p. 552–560.

Enscore, R.E., Biggerstaff, B.J., Brown, T.L., Fulgham, R.F., Reynolds, P.J., Engelthaler, D.M., Levy, C.E., Parmenter, R.R., Montenieri, J.A., Cheek, J.E., Grinnell, R.K., Ettestad, P.J., and Gage, K.L., 2002, Modeling relationships between climate and the frequency of human plague cases in the southwestern United States, 1960–1997: American Journal of Tropical Medicine and Hygiene, v. 66, p. 186–196.

Eskey, C.R., and Haas, V.H., 1940, Plague in the western part of the United States: Public Health Bulletin No. 254, 82 p.

Fenyuk, B.K., 1940, Ecological factors of plague focality: Zoologicheskii Zhurnal (Leningrad), v. 19, p. 349–351.

Fenyuk, B.K., 1948, Ecological factors in natural focality and epizootiology of plague in rodents. A role of secondary hosts of plague, *in* Trudi nauchnoi konferentsii posv'yaschennoi 25 letiu Instituta "Mikrob": Saratov, Russia, p. 37–40.

Gage, K.L., 1998, Plague, *in* Collier, L., Balows, A., Sussman, M., and Hausler, W.J., Jr., eds., Topley and Wilson's microbiology and microbial infections (9th ed.), vol. 3, Bacterial infections: London, Arnold, p. 885–904.

Gage, K.L., and Kosoy, M.Y., 2005, Natural history of plague: perspectives from more than a century of research: Annual Review of Entomology, v. 50, p. 505–528.

Gage, K.L., Ostfeld, R.S., and Olson, J.G., 1995, Nonviral vector-borne zoonoses associated with mammals in the United States: Journal of Mammalogy, v. 76, p. 695–715.

Gage, K.L., Thomas, R.E., and Montenieri, J.A., 1994, The role of predators in the ecology, epidemiology, and surveillance of plague in the United States, *in* Proceedings of the 16th Vertebrate Pest Conference: Davis, University of California, p. 200–206.

Gan, N.V., Voronova, G.A., Yuzvik, L.N., and Belyaeva, V.A., 1990, The capability of *Rhadinopsylla rothschildi* and *R. dahurica* fleas as vectors of plague pathogen in Transbaikal natural focus: Parazitologiya, v. 24, p. 151–154.

Gayskii, N.A., 1944, Infection and immunity in hibernating animals, *in* Izvestiya Irkutskogo Gosudarstvennogo protivochumnogo instituta Sibiri i Dal'nego Vostoka, Irkutsk, v. 5, p. 82–123.

Girard, J.M., Wagner, D.M., Vogler, A.J., Keys, C., Allender, C.J., Drickamer, L.C., and Keim, P., 2004, Differential plague-transmission dynamics determine *Yersinia pestis* population genetic structure on local, regional and global scales: Proceedings of the National Academy of Sciences, v. 101, p. 8408–8413.

Golov, D., and Ioff, I., 1926, Suslik fleas as preservers of plague infection in winter: Reviews Microbiology, Saratov, v. 5, p. 239–251.

Golov, D., and Ioff, I., 1928, On the question of the role of the rodent fleas in the southeastern part of the USSR and the epidemiology of plague, *in* Proceedings of the 1st all-Russian anti-plague conference: Saratov, Mikrob Central Antiplague Institute, p. 102–105.

Gorshkov, O.V., Savostina, E.P., Popov, Y.A., Plotnikov, O.P., Vinogradova, N.A., and Solodovnikov, N.S., 2000, Genotyping *Yersinia pestis* strains from various natural foci: Molekulyarnaya Genetika, Mikrobioliogiya i Virusologiya, issue 3, p. 12–17.

Gratz, N.G., 1999, Rodent reservoirs and flea vectors of natural foci of plague, *in* Plague Manual: Geneva, Switzerland, World Health Organization, p. 63–96.

Guiyoule, A., Grimont, F., Iteman, I., Grimont, P.A.D., Lefevre, M., and Carniel, E., 1994, Plague pandemics investigated by ribotyping of *Yersinia pestis* strains: Journal of Clinical Microbiology, v. 32, p. 634–641.

Hinnebusch, B.J., 1997, Bubonic plague: a molecular genetic case history of the emergence of an infectious disease: Journal of Molecular Medicine, v. 75, p. 645–652.

Hinnebusch, B.J., 2003, Transmission factors: *Yersinia pestis* genes required to infect the flea vector of plague: Advances in Experimental Medicine and Biology, v. 529, p. 55–62.

Hinnebusch, B.J., 2005, The evolution of flea-borne transmission in *Yersinia pestis*: Current Issues in Molecular Biology, v. 7, p. 197–212.

Hinnebusch, B.J., Fischer, E.R., and Schwan, T.G., 1998, Evaluation of the role of the *Yersinia pestis* plasminogen activator and other plasmid-encoded factors in temperature-dependent blockage of the flea: Journal of Infectious Diseases, v. 178, p. 1406–1415.

Hinnebusch, B.J., Perry, R.D., and Schwan, T.G., 1996, Role of the *Yersinia pestis* hemin storage (hms) locus in the transmission of plague by fleas: Science, v. 273, p. 367–370.

Hinnebusch, B.J., Rudolph, A.E., Cherepanov, P., Dixon, J.E., Schwan, T.G., and Forsberg, A., 2002, Role of Yersinia murine toxin in survival of *Yersinia pestis* in the midgut of the flea vector: Science, v. 296, p. 733–735.

Holdenried, R., 1952, Sylvatic plague studies. VII. Plague transmission potentials of the fleas *Diamanus montanus* and *Polygenis gwyni* compared with *Xenopsylla cheopis*: Journal of Infectious Diseases, v. 90, p. 131–140.

Hubbert, W.T., and Goldenberg, M.I., 1970, Natural resistance to plague—genetic basis in the vole (*Microtus californicus*): American Journal of Tropical Medicine and Hygiene, v. 19, p. 1015–1019.

Jarrett, C.O., Deak, E., Isherwood, K.E. Oyston, P.C., Fischer, E.R., Whitney, A.R., Kobayahsi, S.D., DeLeo, F.R., and Hinnebusch, B.J., 2004, Transmission of *Yersinia pestis* from an infectious biofilm in the flea vector: Journal of Infectious Diseases, v. 190, p. 783–792.

Kalabukhov, N.L., 1965, The structure and dynamics of natural foci of plague: Journal of Hygiene, Epidemiology, and Microbiology, v. 9, p. 147–159.

Karimova, T.Y., 2002, Spatial differentiation of natural foci of plague in Sahara-Gobian desert: Uspehi Sovremennoi Biologii, v. 122, p. 422–432.

Kartman, L., 1957, The concept of vector efficiency in experimental studies of plague: Experimental Parasitology, v. 6, p. 599–609.

Kartman, L., and Prince, F.M., 1956, Studies on *Pasteurella pestis* in fleas. V. The experimental plague-vector efficiency of wild rodent fleas compared with *Xenopsylla cheopis*, together with observations on the influence of temperature: American Journal of Tropical Medicine and Hygiene, v. 5, p. 1058–1070.

Kartman, L., Prince, F.M., and Quan, S.F., 1958a, Studies of *Pasteurella pestis* in fleas. VII. The plague-vector efficiency of *Hystrichopsylla linsdalei* compared with *Xenopsylla cheopis* under experimental conditions: American Journal of Tropical Medicine and Hygiene, v. 7, p. 317–322.

Kartman, L., Prince, F.M., Quan, S.F., and Stark, H.E., 1958b, New knowledge of the ecology of sylvatic plague: Annals of the New York Academy of Sciences, v. 70, p. 668–711.

Kartman, L., Quan, S.F., and Lechleitner, R.R., 1962, Die-off of a Gunnison's prairie dog colony in central Colorado. II. Retrospective determination of plague infection in flea vectors, rodents and man: Zoonoses Research, v. 1, p. 201–224.

Keeling, M.J., and Gilligan, C.A., 2000a, Metapopulation dynamics of bubonic plague: Nature, v. 407, p. 903–906.

Keeling, M.J., and Gilligan, C.A., 2000b, Bubonic plague—a metapopulation model of a zoonosis: Proceedings of the Royal Society of London, Series B, v. 267, p. 2219–2230.

Klevytska, A.M., Price, L.B., Schupp, J.M., Worsham, P.L., Wong, J., and Keim, P., 2001, Identification and characterization of variable-number tandem repeats in the *Yersinia pestis* genome: Journal of Clinical Microbiology, v. 39, p. 3179–3185.

Korzun, V.M., and Nikitin, A.I., 1997, Asymmetry of chaetae in fleas *Citellophilus tesquorum* as a possible marker of their capacity for blocking: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 1, p. 34–36.

Kozlov, M., 1979, Plague: natural focality, epizootiology, and epidemic manifestations: Moscow, Meditsina, 192 p.

Kucheruk, V.V., 1965, Paleogenesis of plague natural foci in connection with history of rodent fauna: Fauna i Ekologia Grizunov, v. 7, p. 5–86.

Lechleitner, R.R., Kartman, L., Goldenberg, M.I., and Hudson, B.W., 1968, An epizootic of plague in Gunnison's prairie dogs (*Cynomys gunnisoni*) in south-central Colorado: Ecology, v. 49, p. 734–743.

Lechleitner, R.R., Tileston, J.V., and Kartman, L., 1962, Die-off of a Gunnison's prairie dog colony in central Colorado: Zoonoses Research, v. 1, p. 185–199.

Levi, M.I., 1962, Classification of the varieties of the plague bacillus, *in* Tezisy Dokladov Nauchnoi Konferentsii po Prirodnoi Ochagovosti Chumy i Tularemii, Rostov, p. 72–74.

Levi, M.I., 1994, Gerbils, plague and the Volga (history of one paradox), *in* Levi, M., ed., Zanimatel'nie ocherki o deyatelyah protivochumnoi sistemy Rossii i Sovetskogo Soyuza 1 Informatika: Moscow, Russia, p. 8–44.

Link, V.B., 1955, A history of plague in the United States: U.S. Department of Health, Education and Welfare, Public Health Monograph No. 26, 120 p.

Litvin, V.Y., 1997, Mechanisms of the stable preservation of *Yersinia pestis* in the environment (new facts and hypotheses): Zhurnal Mikrobiologii, issue 4, p. 26–31.

Maevskii, M.P., Bazanova, L.P., and Popkov, A.F., 1999, The survival of the causative agent of plague in the long-tailed suslik from a Tuva natural focus in wintertime: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 1, p. 55–58.

McCoy, G.W., 1908, Plague in ground squirrels: Public Health Reports, v. 23, p. 1289–1293.

Medzykhovsky, G.A., Grazhdanov, A.K., Andryuschenko, V.V., and Tanitovsky, V.A., 2001, The specific features of the spatial and biocenotic structure of a trans-Uralian steppe focus of plague: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 3, p. 39–44.

Mencher, J.S., Smith, S.R., Powell, T.D., Stinchcomb, D.T., Osorio, J.E., and Rocke, T.E., 2004, Protection of black-tailed prairie dogs (*Cynomys ludovicianus*) against plague after voluntary consumption of baits containing recombinant raccoon poxvirus vaccine: Infection and Immunity, v. 72, p. 5502–5505.

Mollaret, H.H., 1963, Conservation expérimentale de la peste dans le sol: Bulletin de la Société Pathologie Exotique, v. 56, p. 1168–1182.

Motin, V.L., Georgescu, A.M., Elliott, J.M., Hu, P., Worsham, P.L., Ott, L.L., Slezak, T.R., Sokhansanj, B.A., Regala, W.M., Brubaker, R.R., and Garcia, E., 2002, Genetic variability of *Yersinia pestis* isolates as predicted by PCR-based IS100 genotyping and analysis of structural genes encoding glycerol-3-phosphate dehydrogenase (glpD): Journal of Bacteriology, v. 184, p. 1019–1027.

Nersesov, V., and Tsikhistavi, G., 1997, On the mechanism of existence of *Yersinia pestis* in nature: Zhurnal Mikrobiologii Moscow, issue 1, p. 102–106.

Nikul'shin, S.V., Onatskaia, T.G., Lukanina, L.M., and Bondarenko, A.L., 1992, Associations of the soil amoeba *Hartmanella rhysodes* with the bacterial causative agents of plague and pseudotuberculosis in an experiment: Zhurnal Mikrobiologii Moscow, issue 9–10, p. 2–5.

Parkhill, J., Wren, B.W., Thomson, N.R., Titball, R.W., Holden, M.T.G., Prentice, M.B., Sebaihia, M., James, K.D., Churcher, C., Mungall, K.L., Baker, S., Basham, D., Bentley, S.D., Brooks, K., Cerdeno-Tarraga, A.M., Chillingworth, T., Cronin, A., Davies, R.M., Davis, P., Dougan, G., Feltwell, T., Hamlin, N., Holroyd, S., Jagels, K., Karlyshev, A.V., Leather, S., Moule, S., Oyston, P.C.F., Quail, M., Rutherford, K., Simmonds, M., Skelton, J., Stevens, K., Whitehead, S., and Barrell, B.G., 2001, Genome sequence of *Yersinia pestis*, the causative agent of plague: Nature, v. 413, p. 523–527.

Parmenter, R.R., Yadav, E.P., Parmenter, C.A., Ettestad, P., and Gage, K.L., 1999, Incidence of plague associated with increased winter-spring precipitation in New Mexico, USA: American Journal of Tropical Medicine and Hygiene, v. 61, p. 814–821.

Perry, R.D., and Fetherston, J.D., 1997, *Yersinia pestis*—etiologic agent of plague: Clinical Microbiology Reviews, v. 10, p. 35–66.

Petrov, V.S., 1959, Natural foci of plague in Eurasia and the principles of their typification: Trudy Sredneaziatskogo Nauchno-Issledovatel'skogo Protivochumnogo Instituta, Alma-Ata, v. 6, p. 3–12.

Petrunina, O.M., 1951, A course of plague infection in great gerbils (*Rhombomys opimus* Licht.) under experimental inoculation: Trudy Sredneaziatskogo Nauchno-Issledovatel'skogo Protivochumnogo Instituta, Alma-Ata, v. 1, p. 17–25.

Poland, J., and Barnes, A., 1979, Plague, *in* Steele, J.H., Stoenner, H., and Kaplan, W., eds., CRC handbook series in zoonoses, Section A—Bacterial, rickettsial, and mycotic diseases, vol. 1: Boca Raton, Fla., CRC Press, p. 515–597.

Poland, J., Quan, T.J., and Barnes, A.M., 1994, Plague, *in* Beran, G.W., ed., CRC handbook series in zoonoses, Section A—bacterial, rickettsial, and mycotic diseases: Boca Raton, Fla., CRC Press, p. 93–112.

Pollitzer, R., 1954, Plague: Geneva, Switzerland, World Health Organization Monograph Series No. 22., 698 p.

Pollitzer, R., 1960, A review of recent literature on plague: Bulletin of the World Health Organization, v. 23, p. 313–400.

Pollitzer, R., and Meyer, K.F., 1961, The ecology of plague, *in* May, J.F., ed., Studies of disease ecology: New York, Hafner, p. 433–501.

Prentice, M.B., James, K.D., Parkhill, J., Baker, S.G., Stevens, K., Simmonds, M.N., Mungall, K.L., Churcher, C., Oyston, P.C.F., Titball, R.W., Wren, B.W., Wain, J., Pickard, D., Hien, T.T., Farrar, J.J., and Dougan, G., 2001, *Yersinia pestis* pFRa shows biovar-specific differences and recent common ancestry with a *Salmonella enterica* serovar typhi plasmid: Journal of Bacteriology, v. 183, p. 2586–2594.

Pushkareva, V.I., 2003, Experimental evaluation of interactions between *Yersinia pestis* EV and soil infusoria and the possibility of the prolonged preservation of bacteria in the protozoan cysts: Zhurnal Mikrobiologii Moscow, issue 4, p. 40–44.

Quan, S.F., Burroughs, A.L., Holdenried, R., and Meyer, K.F., 1953, Studies on the prevention of experimental plague epizootics instituted among mice by infected fleas: Atti del VI Congresso Internazionale di Microbiologia Roma, v. 5, p. 537–540.

Quan, S.F., and Kartman, L., 1956, The resistance of *Microtus* and *Peromyscus* to infection by *Pasteurella pestis*: Transactions of the Royal Society of Tropical Medicine and Hygiene, v. 50, p. 104–105.

Rall, Y.M., 1965, Natural focality and epizootiology of plague: Moscow, Medgiz, 338 p.

Rayor, L.S., 1985, Dynamics of a plague outbreak in Gunnison's prairie dog: Journal of Mammalogy, v. 66, p. 194–196.

Rivkus, Y.Z., Mitropolsky, O.V., Bochkaroff, V.M., Blummer, A.G., and Bochkaroff, S.V., 1993, Desert vegetation as a possible component in plague parasitocoenosis: Bulleten Moskovskogo Obschestva Ispytatelei Prirody, v. 98, p. 3–13.

Rivkus, Y., Ostrovskii, I., Melnikov, I., and Dyatlov, A., 1973, On sensitivity to plague in *Rhombomys opimus* from the northern Kizil-Kum: Problemy Osobo-opasnih Infektsii, Saratov, v. 30, p. 48–58.

Rocke, T.E., Mencher, J., Smith, S.R., Friedlander, A.M., Andrews, G.P., and Baeten, L.A., 2004, Recombinant F1-V fusion protein protects black-footed ferrets (*Mustela nigripes*) against virulent *Yersinia pestis* infection: Journal of Zoo and Wildlife Medicine, v. 35, p. 142–146.

Rotshild, E.V., 2001, Relationship between infectious diseases and concentration of trace metals in the environment and periodic law: Uspehi Sovremennoi Biologii (Moscow), v. 121, p. 251–265.

Seery, D.B., Biggins, D.E., Montenieri, J.A., Enscore, R.E., Tanda, D.T., and Gage, K.L., 2003, Treatment of black-tailed prairie dog burrows with deltamethrin to control fleas (Insecta: Siphonaptera) and plague: Journal of Medical Entomology, v. 40, p. 718–722.

Serzhanov, O.S., Aubakirov, S.A., Ageev, V.S., Matakov, M.I., and Chervyakov, V.D., 1982a, Use of hydrological characteristics for search of places with stable enzootic activity of plague: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 3, p. 80–84.

Serzhanov, O.S., Aubakirov, S.A., Fomushkin, V.M., Ageev, V.S., and Turkpenbaev, H., 1982b, Classification of Central Asian desert plague foci by using hydrothermal indices: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 4, p. 46–50.

Sharets, A.S., Berendyayev, S.A., Krasnikova, L.V., and Tristan, D.F., 1958, The epizootiological effectiveness of one-shot extermination of marmots: Trudy Sredneaziatskogo Nauchno-Issledovatel'skogo Protivochumnogo Instituta, Alma-Ata, v. 4, p. 145–147.

Song, Y., Tong, Z., Wang, J., Wang, L., Guo, Z., Han, Y., Zhang, J., Pei, D., Zhou, D., Qin, H., Pang, X., Han, Y., Zhai, J., Li, M., Cui, B., Qi, Z., Jin, L., Dai, R., Chen, F., Li, S., Ye, C., Du, Z., Lin, W., Wang, J., Yu, J., Yang, H., Wang, J., Huang, P., and Yang, R., 2004, Complete genome sequence of *Yersinia pestis* strain 91001, an isolate avirulent to humans: DNA Research, v. 11, p. 179–197.

Stapp, P., Antolin, M.F., and Ball, M., 2004, Patterns of extinction in prairie-dog metapopulations—plague outbreaks follow El Nino events: Frontiers in Ecology and the Environment, v. 2, p. 235–240.

Stepanov, V.M., 1975, Nutrition factors and their role in manifestation of virulence and immunogenicity of plague pathogen: Saratov, Mikrob Institute Press, 285 p.

Suchkov, I.G., Khidiakov, I.V., Emel'ianenko, E.N., Levi, M.I., Pushkraeva, V.I., Suchko, I.I., Litvin, V., Kulesh, E.V., Zotova, R.S., and Gintsburg, A.L., 1997, The possibility of preserving the causative agent of plague in soil in resting (nonculturable) form: Zhurnal Mikrobiologii, Epidemiologii i Immunobiologii, issue 4, p. 42–46.

Suleimenov, B.M., 2004, Mechanism of plague enzooticity: Almaty, Kazakhstan, Aikembayev's Scientific Center for Quarantinable and Zoonotic Diseases, 234 p.

Suntsov, V.V., and Suntsova, N.I., 2000, Ecological aspects of the evolution of the plague microbe *Yersinia pestis* and the genesis of natural foci: Izvestiya Akademii Nauk, Seriya Biologicheskaya, issue 6, p. 645–657.

Thomas, R.E., Barnes, A.M., Quan, T.J., Beard, M.L., Carter, L.G., and Hopla, C.E., 1988, Susceptibility to *Yersinia pestis* in the northern grasshopper mouse (*Onychomys leucogaster*): Journal of Wildlife Diseases, v. 24, p. 327–333.

Tikhomirov, E., 1999, Epidemiology and distribution of plague, *in* Plague manual: Geneva, Switzerland, World Health Organization, p. 11–41.

Trebesius, K., Harmsen, D., Rakin, A., Schmelz, J., and Heesemann, J., 1998, Development of rRNA-targeted PCR and in situ hybridization with fluorescently labelled oligonucleotides for detection of *Yersinia* species: Journal of Clinical Microbiology, v. 36, p. 2557–2564.

Trudeau, K.M., Britten, H.B., and Restani, M., 2004, Sylvatic plague reduces genetic variability in black-tailed prairie dogs: Journal of Wildlife Diseases, v. 40, p. 205–211.

Tumanskii, V.M., 1957, Classification of the varieties of *P. pestis*: Zhurnal Mikrobiologii Moscow, v. 28, p. 3–7.

Tumanskii, V.M., 1958, Mikrobiologiia chumy (Microbiology of plague) (2d ed.): Moscow, Medgiz.

Ubico, S.R., Maupin, G.O., Fagerstone, K.A., and McLean, R.G., 1988, A plague epizootic in the white-tailed prairie dogs (*Cynomys leucurus*) of Meeteetse, Wyoming: Journal of Wildlife Diseases, v. 24, p. 399–406.

Voronova, G.A., 1989, Enhanced blocking capability of plague microbe in the body of flea: Parazitologiya, v. 23, p. 427–429.

Williams, J.E., and Cavanaugh, D.C., 1983, Chronic infections in laboratory rodents from inoculation of non-encapsulated plague bacilli (*Yersinia pestis*): Experientia, v. 39, p. 408–409.

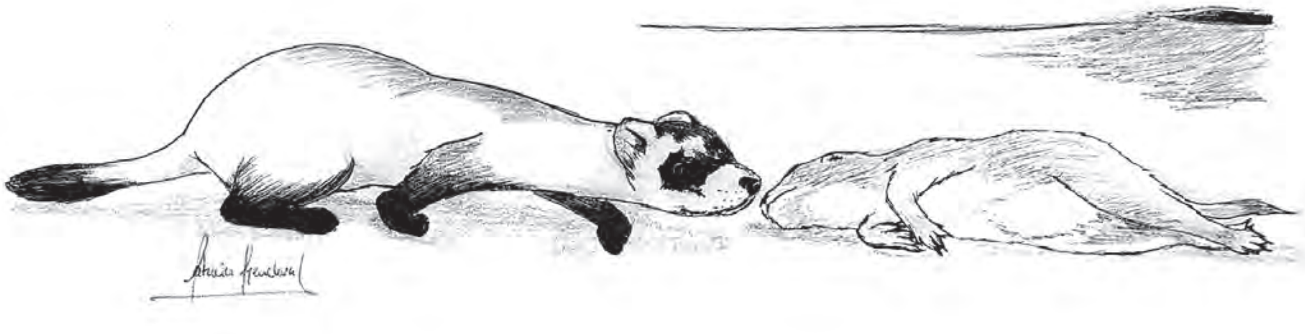
Williams, J.E., Harrison, D.N., and Cavanaugh, D.C., 1975, Cryptic infection of rats with non-encapsulated variants of *Yersinia pestis*: Transactions of the Royal Society of Tropical Medicine and Hygiene, v. 69, p. 171–172.

Williams, E.S., Mills, K., Kwiatkowski, D.R., Thorne, E.T., and Boerger-Fields, A., 1994, Plague in a black-footed ferret (*Mustela nigripes*): Journal of Wildlife Diseases, v. 30, p. 581–585.

World Health Organization, 2004, Human plague in 2002 and 2003: Weekly Epidemiological Record, v. 79, p. 301–306.

Wren, B.W., 2003, The yersiniae—a model genus to study the rapid evolution of bacterial pathogens: Nature Reviews Microbiology, v. 1, p. 55–64.

Zabolotny, D.K., 1915, Pulmonary plague in 1910–1911: Petrograd, Accounts of the Russian Scientific Expedition, 1915.



Exposure of Captive Black-footed Ferrets to Plague and Implications for Species Recovery

By Jerry L. Godbey,[1] Dean E. Biggins,[1] and Della Garelle[2]

Abstract

Plague, a disease caused by the bacterium *Yersinia pestis*, was introduced into North America ca. 1900 and is now common within the ranges of three species of prairie dogs (*Cynomys* spp.) that collectively composed the former range of the highly endangered black-footed ferret (*Mustela nigripes*). An experimental population of black-footed ferrets living in quasi-natural outdoor pens suffered 90 percent mortality after they ate prairie dogs infected with *Y. pestis*. Lethal and sublethal exposure of Siberian polecats (*Mustela eversmannii*) subsequently released into those pens suggested that live *Y. pestis* can be maintained in animal tissues within burrow systems for at least 2 months. A combination of low levels of prairie dog mortality and persistence of *Y. pestis* in dead hosts may pose a chronic hazard for free-ranging black-footed ferrets in areas where plague is enzootic.

Keywords: black-footed ferret, disease, introduced disease, invasive species, *Mustela eversmannii*, *Mustela nigripes*, plague, Siberian polecat, *Yersinia pestis*.

Background

Plague was once believed to be millions of years old, but recent genetic evidence suggests that the causative bacterium, *Yersinia pestis*, may have evolved from *Y. pseudotuberculosis* only 1,500–20,000 years ago (Achtman and others, 1999). The disease has caused devastating epidemics in humans. Plague-like symptoms were recorded in human populations of Asia and Africa as early as 541 A.D. Most scientists believe that plague was introduced into North America from Asia in the late 19th century via rats (*Rattus* spp.) transported by ships (Biggins and Kosoy, 2001). There is now evidence of plague infection in wild mammals or fleas (Insecta: Siphonaptera) from 17 western States in the United States (Gage and Kosoy, this volume).

There are multiple transmission modes for plague, including vector transport (flea bites), aerosol, and consumption of contaminated food items (Gage and Kosoy, this volume). Early cases of plague were linked with rodent infestations and assumed to be from rodent bites, but it was soon recognized that fleas could spread the disease among hosts (Gage, 1998). Aerosol transmission involves expulsion of contaminated droplets of fluid from the lungs of infected animals as they cough; the droplets containing *Y. pestis* may be ingested or inhaled by another potential host. Transmission has also been documented through consumption of infected animals (Gage and Kosoy, this volume). Although some carnivores become infected and do not survive, other species seem quite resistant (Barnes, 1982; Gage and others, 1995).

Plague is common within the ranges of three species of prairie dogs (*Cynomys* spp.) that collectively composed the former range of the highly endangered black-footed ferret (*Mustela nigripes*). The black-footed ferret is extremely dependent on prairie dogs and their colonies (Biggins and Godbey, 2003). Plague causes periodic and sometimes dramatic die-off of prairie dogs, indirectly affecting ferret survival through reduction of prey biomass (Oldemeyer and others, 1993). In 1985, discovery of plague in the white-tailed prairie dogs (*C. leucurus*) supporting the last known population of wild ferrets in Meeteetse, Wyo. (Ubico and others, 1988), caused great concern about the future of ferret habitat. White-tailed prairie dogs were found to be highly susceptible to the disease, but susceptibility of the black-footed ferret was unknown (Williams, 1986). The fears of habitat loss and an unstable prey base proved well founded. A 10-year decline in prairie dogs at Meeteetse left only a remnant population. The initial steep decline of prairie dogs at Meeteetse (fig. 1) was accompanied by a decline in ferrets, which may have been exacerbated by a second disease, canine distemper (Forrest and others, 1988). The dramatic ferret population decline

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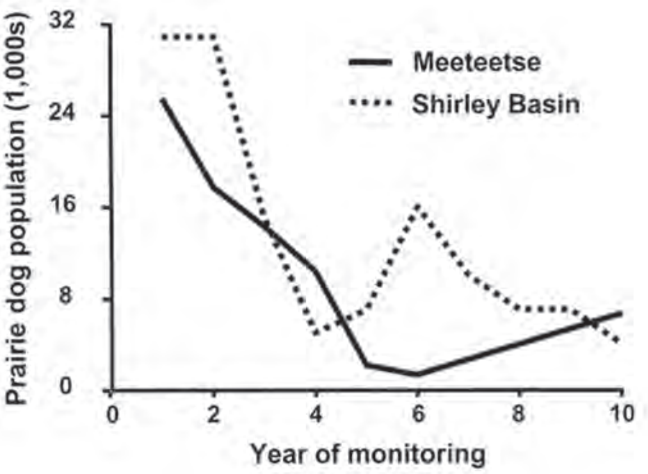

Figure 1. Changes in Wyoming white-tailed prairie dog (*Cynomys leucurus*) populations in areas with known plague. (Adapted from Biggins and Kosoy, 2001. Reprinted with permission of the *Journal of the Idaho Academy of Science*, Pocatello, Idaho.)

prompted the capture of remaining ferrets for captive breeding (Biggins and others, 1997).

The captive breeding program to produce animals for reintroduction into native habitat (i.e., complexes of prairie dog colonies) was ultimately successful (Biggins and Godbey, 2003). Reintroductions of ferrets were begun in 1991 into Wyoming white-tailed prairie dog colonies at Shirley Basin where plague was known to be established. The Shirley Basin population of prairie dogs also declined (fig. 1), but more recently the population has shown some signs of recovery. In 1994, releases of ferrets began in a Montana black-tailed prairie dog (*C. ludovicianus*) complex also known to have plague. Plague has been documented at most reintroduction or potential reintroduction sites, with the exception of those in South Dakota, throughout the ferret range.

Plague was not believed to be a direct hazard to ferrets at the time of the first reintroductions. Williams and others (1991) initially reported that domestic ferrets (*Mustela putorius furo*) and Siberian polecats (*Mustela eversmannii*) were resistant to plague and suggested that “concern about black-footed ferret mortality directly due to *Y. pestis* infection is probably not warranted.” It was therefore surprising to hear of the death of a black-footed ferret due to plague infection (Williams and others, 1994). Williams’s further work with black-footed ferret × Siberian polecat hybrids provided additional evidence on the direct hazard of plague. Nine of 12 hybrids tested became infected and died from ingestion of plague-killed mice; the three survivors failed to show an antibody response (E. Williams, oral commun., 1996). A subsequent trial resulted in 100 percent mortality of four black-footed ferrets exposed to about 800 organisms (equivalent to one flea bite dose) of *Y. pestis* by subcutaneous injection (E. Williams, oral commun., 1999).

Plague Exposure of Captive Black-footed Ferrets at Pueblo

On November 19, 1995, an experimental colony of black-footed ferrets was inadvertently exposed to plague at a research facility housed at the U.S. Army’s Pueblo Chemical Depot, Pueblo, Colo. The facility consisted of modified buildings and enclosures that provided quasi-natural environments for rearing and conditioning black-footed ferrets prior to release. Indoor cages and outdoor pens of various sizes were also used. Outdoor pens consisted of earth-filled structures (fig. 2) with combinations of natural burrows dug by prairie dogs, seminatural burrows constructed of 10.2-cm corrugated plastic drain pipe buried to a depth of about 1 m, and nest boxes. Studies on ferret behaviors were being conducted by using Siberian polecats, black-footed ferrets, and domestic ferrets reared in various environments. There were 64 resident black-footed ferrets in three categories at the time of the exposure. Twenty-three ferrets were assigned to the behavioral studies. Twenty-six ferrets had just been received and were being conditioned as experimental groups for release in Arizona and Montana. Fifteen ferrets 4−7 years old were being held awaiting transfer to zoos as display animals. Most of the black-footed ferrets were provided a diet of prairie dog portions on alternating days; Siberian polecats and domestic ferrets were fed commercial mink chow. The prairie dogs were live-trapped from various sources, quarantined for 10 days, sacrificed, and then frozen until used.

Thirty ferrets were fed on November 19, 1995. The food included portions from five quarantined black-tailed prairie dogs originating in Montana that were removed from one freezer and two nonquarantined Gunnison’s prairie dogs (*C. gunnisoni*) captured from a site near Cortez, Colo., in August

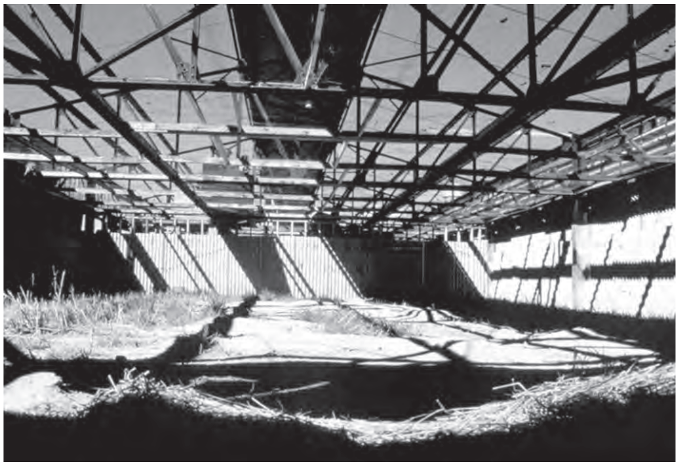

Figure 2. Black-footed ferrets (*Mustela nigripes*) occupied complex burrow systems dug by prairie dogs (*Cynomys* spp.), making them difficult or impossible to locate during and after the outbreak of plague.

1994 and stored in a second freezer. Only the Montana prairie dogs were to be fed, but new animal care personnel were unaware of the distinction. All seven prairie dogs were cut into large pieces on a common cutting board and placed into a bowl for transport to the pens.

Two days after feeding (November 21, 1995), the crew discovered the first obviously ill black-footed ferret in an outdoor pen. The ferret died soon after it was captured. Food-borne disease or poisoning was immediately suspected, so the remaining food was removed, the facilities were quarantined for 10 days, and vitamin K was administered to counteract possible rodenticide poisoning. Ten uneaten or partially eaten pieces of prairie dog were found. Black-tailed and Gunnison's prairie dog parts could not be distinguished because the skin had been removed. The recovered food and the bowl were sent to the Centers for Disease Control (CDC) in Fort Collins, Colo., for testing. Several whole prairie dogs from the Montana shipment and two Gunnison's prairie dogs remaining in the second freezer were also sent to the CDC. Repeated searches of the pens over the next 2 days disclosed other sick and dead ferrets. Clinical signs included lethargy and bloody stools. Of the 30 animals possibly exposed, 19 died and 8 were missing and presumed dead in underground burrows. Black-footed ferret remains were sent to Colorado State University for necropsy, and tissue samples were forwarded to the CDC for plague testing. The three surviving animals were quarantined, and blood was drawn and sent to the CDC.

Three of the 10 recovered prairie dog pieces, the two remaining Gunnison's prairie dogs, and a swab taken from the inner surface of the transport bowl tested positive for plague. There was no evidence of plague in the tested Montana black-tailed prairie dogs. All dead ferrets were positive for plague in one or more tissue samples. Internal organs showed various stages of infection, but all included intestinal hemorrhaging and congested lungs. Clinical signs were consistent with advanced stages of plague.

Labels on recovered freezer bags indicated that the two Gunnison's prairie dogs fed to the ferrets had died during capture or shipment. During 1994 and 1995, former technicians working at the Pueblo facility received several shipments of Gunnison's prairie dogs from Mr. Gay Balfour of Dog Gone, Inc., Cortez, Colo. Mr. Balfour used a modified industrial street cleaning machine with a large vacuum to extract live prairie dogs from their burrows. A small percentage of his catch was injured or killed during capture, and a few prairie dogs may have been dead in the burrow when extracted by the vacuum. These nonquarantined prairie dogs were to be tested later for plague and stored separately from quarantined prairie dogs. One or both of the Gunnison's prairie dogs fed to the ferrets was likely infected with *Y. pestis*. It is unlikely that all 30 black-footed ferrets received Gunnison's prairie dog pieces. We believe the infected portions of Gunnison's prairie dog cross-contaminated the rest of the prairie dog pieces during processing on the cutting board and/or while being carried in the transport bowl.

Surviving ferret #1148 shared a pen with another black-footed ferret (#268) that died from plague. Initial serum samples from #1148 (December 14, 1995) showed no evidence of plague exposure as judged by passive hemagglutination assay; however; surviving ferrets #565 (titer 1:128) and #1508 (titer 1:256) did show evidence of exposure (fig. 3). Ferrets #1508 and #1148 were transferred to reintroduction sites (Montana and Arizona, respectively) before additional blood samples could be taken. Ferret #565 remained at Pueblo, and blood samples were taken at 2-week intervals to follow the immune response. The titer level for ferret #565 increased to 1:2,048 and then diminished to 1:64 over the next 5 months (fig. 3).

Questions arose regarding the persistence of plague underground, and we elected to move some of the resident Siberian polecats from cages to the outdoor pens for exposure testing. On January 23, 1996, 11 male-female pairs of polecats were transferred into pens that had held ferrets that either died or disappeared. We radio tagged the polecats and took baseline serum samples prior to the transfer. Polecats were located each day visually or via radio telemetry. Additional blood samples were taken approximately monthly for 5 months, and irregularly thereafter.

On January 28, 1996, polecat #889 was found dead underground via radio telemetry. Necropsy and tests of tissues indicated plague as the cause of death. The pen had previously housed a black-footed ferret (#1410) whose body was not recovered. On February 13, 1996, polecat #800 carried the partially mummified remains of a formerly missing black-footed ferret (#1471) into a nest box. Subsequent tests of the polecat's blood indicated no evidence of exposure to plague; however, the remains of ferret #1471 were positive for plague.

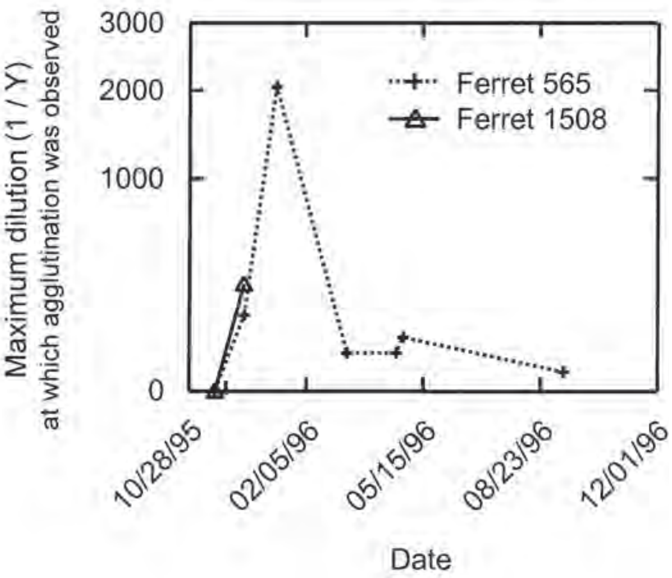

Figure 3. Antibody responses (as determined by passive hemagglutination) of black-footed ferrets (*Mustela nigripes*) #1508 and #565. Estimated date of exposure was 11/19/1995.

On February 23, 1996, polecat #094 recovered the remains of black-footed ferret #636. Serum samples indicated that polecat #094 was positive for plague and remained so for more than 3 months without clinical symptoms (fig. 4). The recovered body of black-footed ferret #636 also tested positive for plague. Siberian polecat #293, housed in a pen where ferret #526 had disappeared, also tested positive for plague. Thus, of the 22 polecats moved to the black-footed ferret pens, 3 tested positive for plague, 1 of which died. One of the seropositive surviving polecats was likely exposed when it recovered the remains of a plague-positive ferret. However, an additional polecat that recovered a plague-positive ferret tested negative. The remaining 18 polecats, including the pen mates of the three that were seropositive for plague, tested negative.

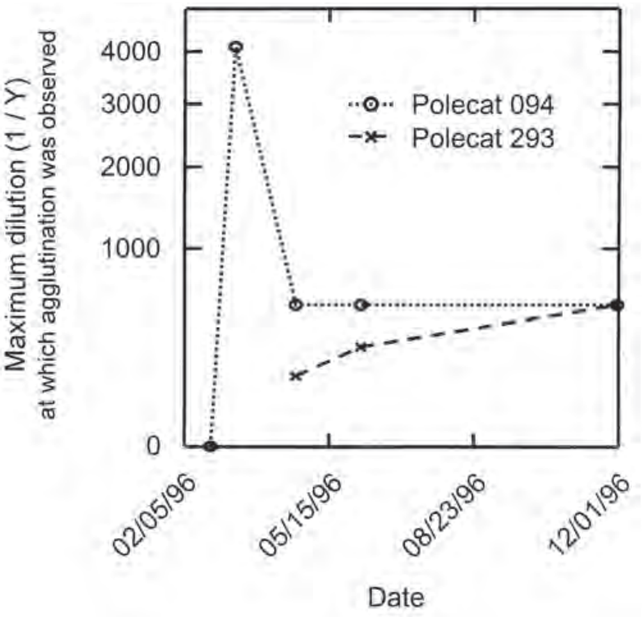

Figure 4. Antibody responses (as determined by passive hemagglutination) of two Siberian polecats (*Mustela eversmannii*) exposed to plague. Earliest potential date of exposure was 1/23/1996, when polecats were moved into pens.

Discussion

Black-footed ferrets may die within 48 hours of consuming plague-infected meat. Of the 30 animals in the group potentially exposed, 27 likely died (some were missing), and 3 survived (2 with antibody responses and 1 with no seroconversion even though its pen mate died of plague). This high rate of mortality was surprising given the circumstances of exposure. Some ferrets apparently ate prairie dog pieces that were surface-contaminated (by mixing with other pieces from infected prairie dogs) and probably received a fairly low dose of *Y. pestis*. Perhaps the two ferrets that survived exposure and showed antibody response consumed very low numbers of bacteria.

Black-footed ferrets are known to scavenge opportunistically; that habit, combined with the fact that plague has been repeatedly detected at most of the black-footed ferret reintroduction sites, suggests that plague-killed rodents constitute a real and eminent hazard for free-ranging black-footed ferrets. Because of the persistence of live *Y. pestis* in carcasses for more than 2 months in relatively cool and humid prairie dog burrows, the hazard may linger long after an epizootic has killed the rodents. If *Y. pestis* resides in prairie dog colonies, occasionally causing disease in individual prairie dogs or other rodents, the risk posed by even widely spaced carcasses could be serious for the relatively mobile foraging ferrets.

Although titers of the Siberian polecats declined, they remained sufficiently high during the course of monitoring (ca. 1 year) to suggest immunity to plague (fig. 4). Because the native habitats of Siberian polecats are centered on Asian foci of plague, these polecats were hypothesized to be more resistant than black-footed ferrets to the disease. Nevertheless, plague killed 88 percent of 33 polecats exposed to *Y. pestis* through subcutaneous injections and consumption of plague-killed mice (Castle and others, 2001), a loss rate similar to the suspected mortality rate for black-footed ferrets (90 percent) in the Pueblo incident.

The initial plague exposure of ferret #565 was more than 3 weeks before the first blood sample was taken on December 14, 1995. The greatest measured antibody response (1:2,048) was on January 11, 1996 (fig. 3), followed by a decline. The relatively low titers after just 3 months may have been insufficient to confer protection against subsequent exposure to plague (fig. 3). Consequently, long-term protection against plague via vaccination may be problematic in black-footed ferrets. More research is clearly needed.

It is unlikely that plague can be eliminated from the wild in North America. Protection of the black-footed ferret from this disease may depend in part on the ability to reduce its spread among and within prairie dog colonies and complexes. The use of pesticides to reduce flea populations provides some hope of reducing plague outbreaks and stabilizing treated areas (Durbian and others, 1997; Karhu and Anderson, 2000; Seery and others, 2003). Repeated dusting of burrows with pesticides, however, is labor intensive and perhaps not practical for large colonies and complexes. If a management tool (e.g., insecticide) can eliminate plague from a prairie dog colony, both ferrets and prey will be afforded some protection. Initial results suggest that flea control may reduce or eliminate epizootics of plague on prairie dog colonies but may not eliminate *Y. pestis* completely. If low levels of enzootic plague remain on such colonies, the threat to ferrets may be substantial, and additional management intervention (e.g., vaccination of ferrets) may be necessary.

Plague is currently common throughout the majority of the black-footed ferret's historical range. Remaining plague-free areas have become vital to reestablishment of the ferret. Why some prairie dog complexes are plague free and how long they will remain so are unknowns. The few remaining plague-free areas provide a unique opportunity to learn about black-footed ferret habitat before plague becomes endemic. As experimental reintroductions and plague research continue, special consideration should be given to existing plague-free areas for recovering the black-footed ferret and for increasing our knowledge of plague dynamics through comparisons of areas with and without the disease.

References Cited

Achtman, M., Zurth, K., Morelli, G., Torrea, G., Guiyoule, A., and Carniel, E., 1999, *Yersinia pestis*, the cause of plague, is a recently emerged clone of *Yersinia pseudotuberculosis*: Proceedings of the National Academy of Sciences, v. 96, p. 14043–14048.

Barnes, A.M., 1982, Surveillance and control of bubonic plague in the United States: Symposia of the Zoological Society of London, v. 50, p. 237–270.

Biggins, D.E., and Godbey, J.L., 2003, Challenges to reestablishment of free-ranging populations of black-footed ferrets: Comptes Rendus Biologies, v. 326 (Suppl. 1), p. S104–S111.

Biggins, D.E., and Kosoy, M.Y., 2001, Influences of introduced plague on North American mammals—implications from ecology of plague in Asia: Journal of Mammalogy, v. 82, p. 906–916.

Biggins, D.E., Miller, B.J., Clark, T.W., and Reading, R.P., 1997, Management of an endangered species: the black-footed ferret, *in* Meffe, G., and Carroll, R., eds., An introduction to conservation biology (2d ed.): Sunderland, Mass., Sinauer Associates, Inc., p. 420–426.

Castle, K.T., Biggins, D.E., Carter, L.G., Chu, M., Innes, K., and Wimsatt, J., 2001, Susceptibility of the Siberian polecat to subcutaneous and oral *Yersinia pestis* exposure: Journal of Wildlife Diseases, v. 37, p. 746–754.

Durbian, F.E., III, Dullum, J., and Matchett, R., 1997, Summary of the 1997 prairie dog flea dusting effort on the Charles M. Russell and UL Bend National Wildlife Refuges and adjacent Bureau of Land Management lands: Lewistown, Mont., U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, 6 p.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Gage, K.L., 1998, Plague, *in* Collier, L., Balows, A., Sussman, M., and Hausler, W.J., Jr., eds., Topley and Wilson's microbiology and microbial infections (9th ed.), vol. 3, Bacterial infections: London, Arnold, p. 885–904.

Gage, K.L., Ostfeld, R.S., and Olson, J.G., 1995, Nonviral vector-borne zoonoses associated with mammals in the United States: Journal of Mammalogy, v. 76, p. 695–715.

Karhu, R.R., and Anderson, S.H., 2000, Effects of pyriproxyfen spray, powder, and oral bait treatments on the relative abundance of fleas (Siphonaptera: Ceratophyllidae) in black-tailed prairie dog (Rodentia: Sciuridae) towns: Journal of Medical Entomology, v. 37, p. 864–871.

Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., 1993, Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, 96 p.

Seery, D.B., Biggins, D.E., Montenieri, J.A., Enscore, R.E., Tanda, D.T., and Gage, K.L., 2003, Treatment of black-tailed prairie dog burrows with deltamethrin to control fleas (Insecta: Siphonaptera) and plague: Journal of Medical Entomology, v. 40, p. 718–722.

Ubico, S.R., Maupin, G.O., Fagerstone, K.A., and McLean, R.G., 1988, A plague epizootic in the white-tailed prairie dogs (*Cynomys leucurus*) of Meeteetse, Wyoming: Journal of Wildlife Diseases, v. 24, p. 399–406.

Williams, E.S., 1986, Experimental infection of white-tailed prairie dogs (*Cynomys leucurus*) with plague (*Yersinia pestis*): Preliminary report to the U.S. Fish and Wildlife Service, Fort Collins, Colo., 11 p.

Williams, E.S., Mills, K., Kwiatkowski, D.R., Thorne, E.T., and Boerger-Fields, A., 1994, Plague in a black-footed ferret (*Mustela nigripes*): Journal of Wildlife Diseases, v. 30, p. 581–585.

Williams, E.S., Thorne, E.T., Quan, T.J., and Anderson, S.L., 1991, Experimental infection of domestic ferrets (*Mustela putorius furo*) and Siberian polecats (*M. eversmanni*) with *Yersinia pestis*: Journal of Wildlife Diseases, v. 27, p. 441–445.

Use of Pesticides To Mitigate the Effects of Plague

By David B. Seery[1,2]

Abstract

On several occasions from 1989 to 2002, burrows within black-tailed prairie dog (*Cynomys ludovicianus*) towns on the Rocky Mountain Arsenal National Wildlife Refuge, Colo., were dusted with a variety of insecticides (carbaryl, permethrin, and deltamethrin) to reduce flea (Insecta: Siphonaptera) abundance in attempts to control plague epizootics. Prairie dog populations were monitored with a combination of various mapping techniques and population abundance indices (visual counts). A single application of deltamethrin significantly reduced populations of the plague vector *Oropsylla hirsuta* and other flea species on prairie dogs and in prairie dog burrows for at least 84 days. A plague epizootic on the Rocky Mountain Arsenal National Wildlife Refuge caused high mortality of prairie dogs on some untreated towns but did not appear to affect nearby towns dusted with deltamethrin. Large-scale relocation efforts followed plague epizootics during the late 1980s and 1990s in an effort to rebuild populations to support wintering eagles and hawks. Between 1989 and 2002, the U.S. Fish and Wildlife Service relocated 12,692 prairie dogs at the Refuge. A comprehensive population monitoring program was instituted in the early 1990s to gage the effectiveness of plague control and relocation. This paper presents a summary of the plague control, relocation, and population monitoring program.

Keywords: black-tailed prairie dog, *Cynomys ludovicianus*, deltamethrin, permethrin, pesticide, plague, *Yersinia pestis*

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) have been intensively managed at the U.S. Fish and Wildlife Service's (FWS) Rocky Mountain Arsenal National Wildlife Refuge (Refuge) since 1986, when a significant bald eagle (*Haliaeetus leucocephalus*) communal winter roost was discovered. Wintering bald eagles feed largely on prairie dogs, through kleptoparasitism of ferruginous hawk (*Buteo regalis*) predations (U.S. Fish and Wildlife Service, 1990). At the Refuge, prairie dogs also provide habitat for burrowing owls (*Athene cunicularia*) and grassland birds, and prey for coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and several species of hawks.

The Refuge is located approximately 16 km northeast of downtown Denver, Colo. Beginning in 1942, the U.S. Army used the site to manufacture chemical and incendiary weapons. After World War II, private companies leased the industrial site for the manufacture of pesticides and herbicides. The Refuge was designated as a Superfund site in 1986 and is currently undergoing environmental remediation. Congress passed legislation in 1992 that established the Refuge upon completion of environmental cleanup. The legislation also states that the Refuge will be managed as if it were a national wildlife refuge during the cleanup. The data collected and analyzed here are part of a larger-scale effort to characterize populations of wildlife at the Refuge. The Refuge currently covers over 6,900 ha in a mosaic of habitat types, including wetland, riparian, and various types and successional stages of grasslands.

Plague (*Yersinia pestis* infection) has periodically affected prairie dog towns on the Refuge since the 1970s. Efforts to control plague during past epizootics involved insecticides, including carbaryl and permethrin dust to control fleas (Insecta: Siphonaptera). Most early efforts were conducted primarily in the interest of public health rather than specifically to protect prairie dogs as important habitat for wildlife species.

Large-scale relocation efforts followed plague epizootics during the late 1980s and 1990s in an effort to rebuild populations to support wintering eagles and hawks. A comprehensive population monitoring program was instituted in the early 1990s to gage the effectiveness of the plague control and relocation program. This paper presents a summary of the plague control, relocation, and population monitoring program, which included mapping active prairie dog colony distribution and visual counts.

Monitoring Distribution and Abundance of Prairie Dogs

Prairie dog colony distribution was determined by using aerial photo interpretation and field verification in all surveys conducted from 1988 to 1993 (Ebasco Services, Inc., 1989; U.S. Fish and Wildlife Service, 1994). Black and white section

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photographs with a scale of approximately 1 cm = 79.2 m were used as field reference guides. Frosted mylar was placed over each section photo, and the boundaries of prairie dogs towns were delineated in the field. Only active prairie dog towns were included in the survey. Mapping was usually conducted in the spring after emergence of prairie dog litters, with some additional mapping at other times of the year to document changes due to plague. Upon completion of the field mapping, the area of each town was determined by using a Radian's Contour Plotting System-1 (CPS-1) for the 1988–90 surveys and an electronic planimeter for the 1991–93 surveys.

Prairie dog town distribution was mapped from 1994 to 2002 by using a TDC1 Global Positioning System (GPS) unit and Pathfinder® software (Trimble Navigation, Ltd., Sunnyvale, Calif.). GPS positions were collected by walking the perimeters of active prairie dog towns and recording positions at 10 to 15 second intervals. The perimeters were determined by outermost active prairie dog burrows or by vegetation clipping (where obvious). GPS data files collected and stored in the rover unit were then downloaded to a computer for subsequent differential analysis. Differential correction (to increase accuracy to 2–5 m) was completed by using community base station files downloaded locally or from the U.S. Forest Service in Fort Collins, Colo. Areas of prairie dog towns were then determined by using Pathfinder software. Final maps were developed with ArcView® software (Environmental Systems Research Institute, Inc., Redlands, Calif.).

Visual counts have been used to estimate populations of white-tailed prairie dogs (*Cynomys leucurus*) and Richardson's ground squirrels (*Spermophilus richardsonii*) and have been shown to correlate well with estimates obtained from mark-recapture data from the same sites (Fagerstone, 1983; Fagerstone and Biggins, 1986; Menkins and others, 1990). Visual counts were chosen as the primary method to estimate population density of black-tailed prairie dogs on the Refuge. This methodology was developed by the FWS's National Ecology Research Center (now the Fort Collins Science Center, U.S. Geological Survey) in Fort Collins, Colo., to evaluate black-footed ferret habitat (Biggins and others, 1993). Study plots of various sizes were established (depending on time, personnel, and suitability of habitat constraints), and in some cases entire prairie dog towns were counted. Visual counts were conducted for 3 consecutive days on each plot, starting approximately 30 minutes after sunrise and continuing (with 15 minutes between counts) until prairie dog numbers began to decrease, usually midmorning. The highest individual count of prairie dogs recorded during the 3 days was then used to determine the density of each plot (highest count/area). Densities were then summed and divided by the number of plots to determine the mean density for each year.

History of Plague at the Refuge

Early efforts to control plague at the Refuge began in the mid-1970s. Carbaryl insecticide was infused into prairie dog burrows in an effort to control fleas and the spread of plague in the central portion of the Refuge. Primary attention was given to prairie dog towns located close to areas of human activity. Other than a few general statements and a hand-drawn map of the area, this plague epizootic was not well documented. The duration and extent of the epizootic and the effectiveness of the treatment are unknown.

The next recorded plague event started in November 1988 in the northeast corner of the Refuge. Mapping of prairie dog towns on the Refuge had just been completed (October 1988) in response to the discovery of a communal bald eagle winter roost in 1986. Due to the importance of prairie dogs as a food source for wintering bald eagles, increased attention was given to controlling this epizootic. Plague rapidly spread through a large (>600 ha) prairie dog town on the eastern portion of the Refuge and reached the southeast corner of the refuge in 20 days (J. Harrison, oral commun., 1994).

Previous studies have indicated that permethrin dust was effective at reducing fleas in burrows and on prairie dogs (Beard and others 1992; Barnes, 1993). A large quantity of permethrin powder was obtained and applied in prairie dog burrows in attempts to control plague, mostly in the interest of public health. The plague epizootic continued through September 1989, reducing prairie dog towns on the Refuge by 95 percent. Although the effects of plague on prairie dog towns was well documented during this event, the techniques involved with application of permethrin powder were not. It is believed that application rates were as suggested on the product label (1–2 oz/burrow) and that pressurized applicators were used. It is unknown, however, when and where (before, during, or after the passage of plague, or in active or inactive towns) the powder was applied. This lack of information hindered development of strategies to control future epizootics.

A prairie dog relocation program began in August 1989 (table 1). A standardized approach to prairie dog relocation techniques was developed in order to maximize efficiency and success of the relocation efforts. The FWS developed cooperative agreements with several private relocator groups from the Denver area. These groups were composed of private citizens who advocated saving prairie dog towns from destruction caused by the rapid growth of urban development. Prairie dogs were collected for relocation by a number of methods, including water flushing, vacuum truck, and live trapping.

Following the large-scale and successful relocation program (tables 1 and 2; 6,842 prairie dogs relocated through 1993, yielding >980 ha of active prairie dog towns in 1994), plague once again hit in May 1994, starting in the northeastern portion of the Refuge. The progression of this epizootic followed the same path as the one in 1988–89, proceeding south and east through a large (>400 ha) town on the east side of the Refuge. Several attempts were made to halt the advance of plague by dusting with permethrin powder on active portions of prairie dog towns in advance of the epizootic. Visual observation of prairie dogs above ground was used to determine where to begin dusting and to map the extent of plague. Plague continued to advance (much as wildfire spreads), slowing in its progress for several days to a few

Table 1. Summary of black-tailed prairie dog (*Cynomys ludovicianus*) relocations at Rocky Mountain Arsenal National Wildlife Refuge from 1989 to 2002.

	Source		
Year	On refuge	Off refuge	Total
1989	132	579	711
1990	447	2,525	2,972
1991	252	2,125	2,377
1992	229	438	667
1993	48	67	115
1994	175	0	175
1995	276	140	416
1996	43	1,711	1,754
1997	207	1,659	1,866
1998	269	502	771
1999	90	0	90
2000	208	0	208
2001	261	0	261
2002	309	0	309
Total	2,946	9,746	12,692

weeks as it encountered dusted areas, but eventually continuing to spread to all areas of the prairie dog town. By the fall of 1994, plague had decimated approximately 695 ha (or about 70 percent of the area occupied in May 1994) and had moved to the western portion of the Refuge. Plague continued throughout the winter. By the following spring, only about 73 ha of active prairie dog towns remained, and by September 1995, only 9 ha of active prairie dog towns remained (table 2). The second large-scale relocation program began shortly thereafter, and by the time this effort was winding down in 1998, over 4,000 prairie dogs had been relocated onto the Refuge from outside sources. The population rebounded quickly, reaching over 350 ha of active prairie dog towns after relocation of 5,072 prairie dogs (table 1), and continuing to grow to over 660 ha by 2000 (table 2), when the next epizootic arrived.

In January 2000, inspection of a prairie dog town at the northeast corner of the Refuge revealed no living prairie dogs. A plague control program was instituted immediately, with crews applying 35.9 kg of permethrin powder on about 40 ha of prairie dog towns within 1.6 km of the plague site by February 2, 2000. No other plague activity was observed on the Refuge until April 18, 2000, when a contractor working on a nearby remediation project found a dead prairie dog approximately 1.6 km from the earlier outbreak of plague. The carcass was sent to the Centers for Disease Control (CDC), and plague was confirmed on April 19, 2000. The plague control program was started again on April 20, 2000, concentrating on towns within 1.6 km of where the carcass had been found. Additional dead prairie dogs were found during May 2000 (plague positive), and the scope of plague control was expanded. By the end of June 2000 all active prairie dog towns in adjoining sections (about 51 ha) were dusted.

During the course of this epizootic, a product evaluation study on Deltadust® (Aventis Environmental Health, Montvale, N.J.) began. Deltadust (a powdered formulation of deltamethrin) is a relatively new product containing a synthetic pyrethroid similar to permethrin and is reportedly waterproof, providing insecticidal action for up to 8 months. From July to October 2000, the FWS, assisted by plague lab personnel from the CDC in Fort Collins, Colo., evaluated Deltadust at the Refuge. The results of the study (Seery and others, 2003) indicated Deltadust was effective at reducing flea populations within prairie dog burrows and had a residual effect over 84 days posttreatment. No toxic effects were noted in the prairie dog population from application of Deltadust into the burrows. After initial results were obtained from this study, additional quantities of deltamethrin were obtained and used immediately in attempts to control the continued spread of the epizootic. From July to October 2000, approximately 46 ha of high priority prairie dog towns (important to wintering bald eagles, public use areas, burrowing owl breeding areas, etc.) were treated with deltamethrin. All of these sites were monitored over the winter (2000–01). The treated sites survived without any sign of plague whereas most of the areas dusted with permethrin had succumbed to plague. However, plague activity was observed again in the spring of 2001 (based on plague-positive carcasses) in limited, widely dispersed areas across the Refuge. Populations of prairie dogs on several, but not all, of the towns dusted with deltamethrin in the summer and fall of 2000 were eventually decimated from plague during 2001, 6 to 10 months after towns were treated.

Discussion of Plague Management

From 1988 to 2001, a variety of insecticides (carbaryl, permethrin, and deltamethrin) were used at the Refuge in attempts to control plague in prairie dogs. Early attempts were aimed mostly at providing protection in areas heavily used by humans and were generally ineffective at controlling plague in prairie dogs. By 1994, more emphasis was given to providing protection to the prairie dogs themselves and even attempting to stop the spread of plague. In some cases, when applied early, these actions were successful in halting the spread of plague. On the Refuge, studies also indicated significant flea reductions after burrows were dusted with permethrin, although flea numbers on prairie dogs returned to previous levels 10 to 18 days posttreatment (Karhu and Anderson,

Table 2. Black-tailed prairie dog (*Cynomys ludovicianus*) population estimates at Rocky Mountain Arsenal National Wildlife Refuge, 1988–2002. Three major plague epizootics occurred in prairie dogs on the Refuge: 1988–89, 1994–95, and 2000–02.

Year	Prairie dogs/ha (mean ± SE)	*n* (plots)	Area occupied (ha)	Estimated population	r[a]
1988[b]	20.2 ± 1.6	24	1,850.8	37,406	----
1989[b]	20.2[c]	---	99.8	2,017	-2.92
1990[b]	12.2 ± 2.0	6	232.9	2,842	0.343
1991	14.6 ± 1.08	10	555.56	8,134	1.05
1992	17.8 ± 1.79	12	663.27	11,793	0.371
1993	22.57 ± 1.77	12	737.05	16,636	0.344
1994	23.47 ± 1.31	10	982.75	23,065	0.327
1995 (May)	50.86 ± 9.49	9	72.86	3,708	-1.83
1995 (Sept.)	50.86 ± 9.49	9	9.0	458	-2.09
1996	41.16 ± 5.6	8	35.9	1,478	1.17
1997	54.8 ± 10.8	6	139.77	7,640	1.64
1998	32.8 ± 3.78	10	357.77	11,735	0.429
1999	24.5 ± 4.41	10	533.74	13,076	0.108
2000	----	----	666.75	----	----
2001 (May)	----	----	250.43	----	----
2001 (Oct.)	----	----	105.0	----	----
2002	28.4 ± 4.31	15	127.02	3,607	----

[a] r = per capita growth rate, ln[N(t+1)/N(t)].

[b] 1988–90 data from Stollar and Associates (1992).

[c] No data available, density estimated.

2000). At the "ball field" prairie dog town, for example, the application of permethrin dust in a timely manner saved a prairie dog town used for environmental education programs. This town, located west of the administration complex on the Refuge, was a popular stop for school groups on tours of the Refuge. On July 8, 1995, Refuge personnel found a dead prairie dog at the site. The carcass was sent to the CDC in Fort Collins, Colo., for testing. After receiving confirmation of plague, the entire prairie dog town was dusted (0.68 ha) with permethrin on July 12, 1995. No other prairie dog carcasses were found during that time. That town was used during visual counts (June) to estimate abundance, so the population was known (*n* = 77). Over the course of the next month, periodic visual counts were made to monitor effectiveness of the treatment. After a month the population stabilized at about 25 prairie dogs, a loss of about two-thirds of the population. There were no other signs of mortality from plague at the site over the next several years, and the population began a gradual rebound, growing to cover 7.3 ha by 2001.

It appears that Deltadust, when applied in the manner described by Seery and others (2003), significantly reduces flea populations within prairie dog burrow systems and on prairie dogs. Deltamethrin has a significant residual effect, with flea populations still at nondetectable levels by day 84. Cessation of mortality of prairie dogs following application of deltamethrin accompanied flea reductions caused by the treatment. By comparison, previous studies evaluating permethrin dust have reported low numbers of fleas after 84 days (Beard and others, 1992).

Deltamethrin represents an effective alternative to permethrin dust for controlling flea populations in prairie dog towns. Its relative effectiveness, ease of application, and safety should make it an important tool for managing plague epizootics in these animals. The long residual activity of deltamethrin suggests that single applications may reduce fleas throughout most of the season of plague activity, which typically occurs during the warmest 4 to 5 months of the year. These advantages also suggest that deltamethrin can be useful for protecting prairie dogs as an important habitat component for raptors and other carnivores, such as black-footed ferrets, at wildlife conservation locations (for wintering, breeding, and translocation).

References Cited

Barnes, A.M., 1993, A review of plague and its relevance to prairie dog populations and the black-footed ferret, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 28–37.

Beard, M.L., Rose, S.T., Barnes, A., and Montenieri, J., 1992, Control of *Oropsylla hirsuta*, a plague vector, by treatment of prairie dog burrows with 0.5% permethrin dust: Journal of Medical Entomology, v. 29, p. 25–29.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Ebasco Services, Inc., 1989, Black-tailed prairie dog—activity survey interim report: Prepared for the U.S. Army Program Manager's Office for the Rocky Mountain Arsenal Contamination Cleanup.

Fagerstone, K.A., 1983, An evaluation of visual counts for censusing ground squirrels, *in* Kaukeinen, D.E., ed., Vertebrate pest control and management materials, fourth symposium: Philadelphia, Pa., American Society for Testing and Materials, ASTM ATP 817, p. 239–246.

Fagerstone, K.A., and Biggins, D.E., 1986, Comparison of capture-recapture and visual count indices of prairie dog densities in black-footed ferret habitat: Great Basin Naturalist, v. 8, p. 94–98.

Karhu, R.R., and Anderson, S., 2000, Effects of pyriproxyfen spray, powder, and oral bait treatments on the relative abundance of fleas (Siphonaptera: Ceratophyllidae) in black-tailed prairie dog (Rodentia: Sciuridae) towns: Journal of Medical Entomology, v. 37, p. 864–871.

Menkins, G.E., Biggins, D., and Anderson, S., 1990, Visual counts as an index of white-tailed prairie dog density: Wildlife Society Bulletin, v. 18, p. 290–296.

Seery, D.B., Biggins, D.E., Montenieri, J.A., Enscore, R.E., Tanda, D.T., and Gage, K.L., 2003, Treatment of black-tailed prairie dog burrows with deltamethrin to control fleas (Insecta: Siphonaptera) and plague: Journal of Medical Entomology, v. 40, p. 718–722.

Stollar and Associates, 1992, Biota annual monitoring report for 1990 and summary report for 1988 to 1990, comprehensive monitoring program, final report: Prepared for Rocky Mountain Arsenal Field Office, U.S. Fish and Wildlife Service, 16 p.

U.S. Fish and Wildlife Service, 1990, Annual Progress Report: Commerce City, Colo., Rocky Mountain Arsenal Field Office, 177 p.

U.S. Fish and Wildlife Service, 1994, Annual Progress Report: Commerce City, Colo., Rocky Mountain Arsenal Field Office, 182 p.

Vaccination as a Potential Means To Prevent Plague in Black-footed Ferrets

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Abstract

This study was conducted to further assess the feasibility of vaccinating black-footed ferrets (*Mustela nigripes*) against plague (caused by the bacterium *Yersinia pestis*). On days 0 and 28, 17 postreproductive ferrets were immunized by subcutaneous injection with a recombinant fusion protein containing F1 and V antigens from *Y. pestis*. Another 17 animals received a placebo by the same route. Two weeks after the second immunization, mean antibody titers to *Y. pestis* F1 and V antigens were measured and found to be significantly higher in vaccinates than their preimmunization values ($P < 0.0001$) and significantly higher than the control values ($P < 0.0001$). Six months postimmunization, 16 vaccinates and eight controls were challenged with approximately 8,000 colony forming units of virulent plague by subcutaneous inoculation. Eleven of 16 vaccinates (69 percent) survived with no ill effects whereas all eight control animals died within 3–6 days. Two months later, the 11 surviving vaccinates were challenged again by ingestion of a plague-infected mouse. None of the animals showed any ill effects and all survived. In contrast, seven control ferrets fed infected mice died within 2–4 days, including one animal that did not actually ingest the mouse but was likely exposed to it. This study demonstrates that immunization of ferrets with the recombinant F1-V fusion protein can induce significant antibody responses and reduce their susceptibility to plague infection.

Keywords: black-footed ferrets, immunization, *Mustela nigripes*, sylvatic plague, vaccine, *Yersinia pestis*

Introduction

Sylvatic plague, caused by the bacterium *Yersinia pestis*, is primarily a disease of wild rodents that is transmitted between mammals via flea (Insecta: Siphonaptera) bite, direct contact, ingestion, or inhalation. Since its introduction into the United States in the early 1900s, plague has become firmly established in native rodent populations throughout the West, causing frequent epizootics (Barnes, 1993). For many species of wildlife, plague mortality has become a serious conservation issue. Over half of the North American rodent species of conservation concern (Hafner and others, 1998), including several species of prairie dogs (*Cynomys* spp.), reside within the range of plague in western North America (Barnes, 1982). In addition, the endangered black-footed ferret (*Mustela nigripes*), which relies almost exclusively on prairie dogs for food and shelter, is highly susceptible to plague and suffers high mortality upon infection (Williams and others, 1994; Rocke and others, 2004).

Current methods to control plague in prairie dog colonies include dusting burrows with insecticides after the onset of an epizootic and population reduction. Although these methods have limited success in controlling outbreaks in rodents, they may be applied too late to be effective for ferrets, and population reduction is inappropriate for an endangered species. Recent studies have shown that multiple doses of a recombinant vaccine, consisting of two fused plague antigens, F1 and V (F1-V protein), protect laboratory mice against the bubonic or pneumonic form of plague (Heath and others, 1998). In a pilot study conducted at the U.S. Geological Survey's National Wildlife Health Center (NWHC) in Madison, Wis., six of seven ferrets that received a three-dose regimen of F1-V protein via subcutaneous injection survived challenge with 7,800 colony forming units (CFU) of *Y. pestis* 3 weeks after their last booster dose (Rocke and others, 2004). The objectives of the study described herein were to assess vaccine efficacy with a larger group of animals and with a longer duration between vaccination and challenge (6 months).

Methods

Thirty-four ferrets (23 females and 11 males) were selected for this study at the U.S. Fish and Wildlife Service,

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National Black-footed Ferret Conservation Center (NBFFCC), Wheatland, Wyo. (now located near Wellington, Colo.), where the initial immunization and collection of baseline blood samples took place. All animals were 3–4 years of age and had been vaccinated previously against rabies and canine distemper. At the NBFFCC, animals were marked individually with subcutaneous embedded microchips (AVID® Microchip I.D. Systems, Folsom, La.) and housed individually in 2.5-cm wire-mesh cages (61 x 61 cm) with vinyl floors. Wooden nest boxes (45 x 22 x 28 cm) were attached to the exterior of the cages via 30-cm corrugated drain pipe. Bedding consisted of absorbent cellulose (ALPHA-dri™; Shepherd Specialty Papers, Watertown, Tenn.). The animals were fed 60–70 g of a raw horsemeat diet (Toronto Zoo Small Carnivore Diet; Milliken Meat Products, Ltd., Scarborough, Ontario, Canada) once daily. Water was provided ad libitum in ceramic bowls or sipper bottles.

For challenge experiments, all ferrets were transported to the NWHC where they were placed in a Biosafety Level 3 animal holding facility. Upon arrival, the animals were treated prophylactically for coccidiosis and housed individually in stainless steel cages as described previously (Rocke and others, 2004). The animals were fed Toronto Zoo Small Carnivore Diet or Dallas Crown Carnivore Diet (Dallas Crown, Inc., Kaufman, Tex.) when the Toronto Zoo Small Carnivore Diet was unavailable. Methods of anesthesia and blood sampling were described in Rocke and others (2004).

This study was reviewed and approved by NWHC's Animal Care and Use Committee and Biosafety Committee. All personnel handling plague-infected animals or carcasses were required to wear powered, air-purifying (Hepa-filtered) respirators with fullface shields, rubber aprons and boots, and double surgical gloves. In addition, personnel collecting and handling animals and conducting necropsies were required to take prophylactic antibiotics (as prescribed by occupational health physicians).

On days 0 and 28, 17 ferrets at NBFFCC received 0.5 mL F1-V vaccine-adjuvant preparation (100 µg of antigen) by subcutaneous injection between the scapulae. The F1-V fusion protein and our methods of preparing the vaccine have been described previously (Heath and others, 1998; Rocke and others, 2004). Seventeen control animals received a placebo of 0.5 mL of Dulbecco's Medium (Sigma Chemical Co., St. Louis, Mo.). One control animal was euthanized due to disease unrelated to vaccination; the rest were transported to NWHC the 12th week postvaccination where they were held in isolation for several months prior to plague challenge. During this period, two other animals (one vaccinate and one control) were euthanized due to disease issues unrelated to vaccination. The control animal had severe abscessation and edema of the neck region from which *Streptococcus zooepidemicus* was isolated. The vaccinate experienced acute, medically nonresponsive hind limb paresis. Upon histological examination, both animals were found to have kidney lesions (tubular nephrosis and glomerulopathy).

Six months postvaccination (day 178), six vaccinates and eight controls were challenged with 7,800 CFU of our *Y. pestis* challenge stock (CO92) described previously (Rocke and others, 2004); the bacteria were administered in 0.2 mL sterile saline by subcutaneous injection in the scapular region. Blood samples were taken from animals prior to first vaccination and on days 28, 42, and 167. Animals were monitored daily for signs of illness, and day of death was noted; severely debilitated animals were euthanized by CO_2 asphyxiation.

To determine if survivors were protected from further plague infection, the 11 vaccinated ferrets surviving 2 months after the initial subcutaneous challenge were bled to determine titers to plague antigens, and each was then orally challenged with a single plague-infected mouse; seven unvaccinated ferrets each fed a single infected mouse served as controls. For the oral challenge, 6-week-old mice were inoculated with a 0.1-mL volume of >4,000 CFU *Y. pestis* by intradermal injection. Upon death within 3 days after challenge, the mice were placed in the cage of each ferret. Any carcasses or parts of carcasses not ingested by ferrets within 3–4 hours were removed and discarded. Any ferrets surviving the second challenge were bled to determine antibody titers after 4 weeks and then euthanized by intracardiac injection of euthanasia solution (Euthasol; Delmarva Laboratories, Midlothian, Va.). In both experiments, dead or euthanized ferrets were immediately necropsied. Selected tissues were collected for bacterial isolation (Rocke and others, 2004) and histology.

Serology

Blood samples were collected in sterile glass serum separator tubes from all animals prior to immunization, boost, and challenge. Survivors were also bled after challenge. After centrifugation of blood samples, the serum was transferred to 2-mL polypropylene tubes and frozen at -20ºC for future analyses. Antibodies against F1 and V antigens were measured by using an enzyme-linked immunosorbent assay (ELISA) as previously described (Rocke and others, 2004).

Statistical Analysis

Antibody titers were transformed by calculating the $\log_{10}$ of the reciprocal titer value. Change in titer was then calculated by subtracting an individual animal's transformed preinoculation anti-F1 or anti-V titer from the transformed titer of each of that same animal's subsequent blood samples. Statistical difference in change of titer between groups was tested separately at each blood sampling period by using a one-tailed Mann-Whitney test at $P = 0.05$ (Zar, 1999). Difference in survivorship between groups was tested at $P = 0.05$ by using the Fisher Exact test (Zar, 1999), and days to death were compared by using a one-tailed Mann-Whitney test at $P = 0.10$.

Results

All 17 F1-V vaccinated ferrets developed significant antibody titers to both F1 and V antigens after immunization. In contrast, antibody titers of control animals remained negative. Geometric mean titers in anti-F1 and anti-V antibody increased significantly after the initial dose of vaccine was administered ($P < 0.0001$) and increased to even higher levels (means of 1:25,000 and 1:40,000, respectively) after the second dose, or boost ($P < 0.0001$) (fig. 1). Within 6 months, the mean anti-F1 and anti-V titers of vaccinates declined significantly ($P = 0.0004$ and $P < 0.0001$, respectively), although they were still significantly higher than their prevaccination titers ($P < 0.0001$) and the unvaccinated controls prior to challenge ($P < 0.0001$).

Eleven of the 16 vaccinated ferrets that were inoculated with *Y. pestis* survived the subcutaneous challenge and showed no signs of illness. The other five vaccinates became sick and died with an average time to death of 9.4 days. The first vaccinate died on day 4 with unusual gross lesions, including bloody diarrhea, multifocal hemorrhage throughout the intestines, and swollen kidneys. *Yersinia pestis* was isolated in low numbers from the spleen, and *S. zooepidemicus* was also isolated from the retropharyngeal lymph node. The three vaccinates that died on days 7 and 9 had gross lesions more consistent with unvaccinated controls (enlarged and slightly hemorrhagic lymph nodes, enlarged spleen, mottled lungs), and *Y. pestis* was isolated from numerous tissues from all three carcasses. The last vaccinate died on day 18 postchallenge. No *Y. pestis* was isolated from any tissue, but *S. zooepidemicus* was found in the spleen, lymph nodes, liver, lungs, heart, esophagus, and an abscessed region on the neck. In comparison, all eight unvaccinated controls inoculated with *Y. pestis* died within 3–6 days of challenge, with an average time to death of 4.3 days. All had gross lesions consistent with plague infection, and large numbers of *Y. pestis* were isolated from the tissues of all animals. Including the animals that had *S. zooepidemicus*, the survival rate of vaccinates was significantly higher than that of controls ($P = 0.02$), and time to death was significantly longer ($P = 0.02$). At the time of subcutaneous challenge, the mean anti-F1 titer of vaccinates that survived (9,030) was not significantly higher ($P = 0.165$) than that of vaccinates that died (5,580). The mean anti-V titer was significantly higher ($P = 0.035$), however, in surviving vaccinates (16,950) compared to those that died (9,030).

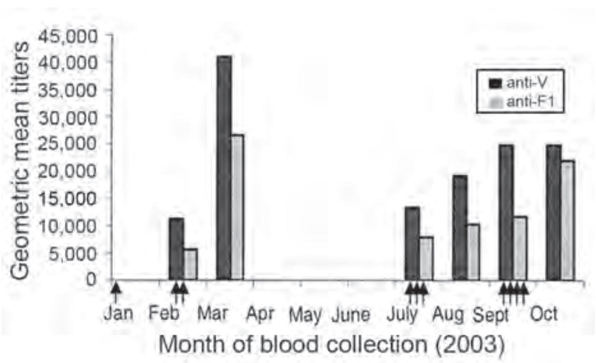

Figure 1. Geometric mean anti-F1 and anti-V antibody titers in black-footed ferrets (*Mustela nigripes*) immunized with F1-V protein. The dates of the first and second vaccinations (prime and boost), first subcutaneous challenge with *Yersinia pestis*, and second challenge via ingestion of infected mice are indicated with 1 arrow, 2 arrows, 3 arrows, and 4 arrows, respectively.

Two months after the subcutaneous challenge, the 11 surviving vaccinates received a second plague challenge via consumption of a plague-infected mouse. Each of them consumed an entire infected mouse, and all survived with no apparent clinical signs. In contrast, the seven control animals presented with infected mice all died within 2–4 days, including one animal that did not ingest its mouse but presumably licked or sniffed it; this animal died on day 4. *Yersinia pestis* was isolated from most of the controls, with the exception of one that died on day 2 that had an overwhelming infection of *S. zooepidemicus*.

Discussion

In this study, the majority (69 percent) of vaccinated ferrets survived subcutaneous plague challenge 6 months post-immunization in contrast to the unvaccinated controls that all died of the infection. These results are similar to those of our previous pilot study in which six of seven (86 percent) vaccinated ferrets survived subcutaneous challenge with the same dose of *Y. pestis* (Rocke and others, 2004). In that study, however, ferrets received an extra boost of F1-V just 3 weeks prior to challenge in a three-dose regimen whereas in the present study, the animals received only two doses and were not challenged with the bacteria until 6 months later. Mean anti-F1 and anti-V antibody titers of immunized animals increased significantly after vaccination, particularly after the boost; however, they decreased over the next several months to nearly preboost titers. Vaccinates that survived subcutaneous challenge had a slightly higher mean anti-V titer than those vaccinates that succumbed to the same challenge.

In nature, ferrets are likely exposed to plague by several means. They may be bitten by infected fleas as they navigate through burrows or as they feed on prairie dogs. It is also highly likely that ferrets contract plague while feeding on infected prairie dogs through either direct contact or inhalation of the bacteria. The one unvaccinated ferret in our study that contracted plague and died within 4 days even though it declined to consume the infected mouse is evidence of their extreme susceptibility to the bacteria via this route. Interestingly, in this study vaccinated ferrets that survived an initial subcutaneous challenge with *Y. pestis* all survived ingestion of an infected mouse 2 months later. This result suggests that flea-bite exposure of vaccinated ferrets in nature could potentially boost their immune response enough to ward off further plague infection via consumption of infected prey. We suspect that some vaccinated ferrets would also survive an initial oral challenge with infected mice. In a previous pilot study, two of five vaccinated ferrets survived after ingestion of infected mice as an initial challenge (T. Rocke, unpub. data, 2001). These results are promising but insufficient, so we are currently exploring methods for boosting mucosal immunity in vaccinates.

At least four ferrets in this study were found to have *S. zooepidemicus* infections, one prior to challenge and three after challenge. In addition, three other ferrets had kidney lesions (glomerulonephritis) visible upon histologic examination of tissues that may have resulted from a previous infection (T. Rocke, unpub. data, 2003). Kidney damage is a reported sequela to *S. zooepidemicus* infection in humans (Barnham and others, 1983; Francis and others, 1993; Pinto and others, 2001) and horses (Divers and others, 1992). Raw horsemeat has been a documented source of *S. zooepidemicus* for other small carnivorous mammals, including short-nosed bandicoots (*Isoodon macrourus*) and shrews (*Tupaia glis* and *Elephantulus rufescens*) (Shaw and others, 1984) and several primate species (Schiller and others, 1989). In our study, ferrets were fed raw horsemeat diets from two different sources, both at NBFFCC and NWHC. Samples of the meat were cultured after the infection was diagnosed, but the bacterium was not isolated. Even though the source of infection is still unknown, we believe many of our study animals may have had underlying *S. zooepidemicus* infections or were recovering from an infection. This bacterium may have significantly impacted the ability of vaccinated ferrets to withstand challenge to *Y. pestis*.

Summary

The results of this study suggest that two doses of the F1-V protein are sufficient to reduce ferret mortality from subcutaneous injection of plague for at least 6 months postimmunization, even in the face of a chronic, underlying *Streptococcus* infection. We suspect that vaccination of younger animals (<1 year old) and animals that are less stressed would result in even higher antibody titers, better resistance to the disease, and longer duration of immunity. Until other methods of plague control are developed, the F1-V vaccine could protect ferrets in captive breeding facilities and animals intended for release programs. Black-footed ferret kits and dams in captive breeding programs are fed wild prairie dogs that are captured, quarantined, and killed for that purpose. However, the loss of numerous captive ferrets at one facility from ingestion of plague-infected prairie dog meat demonstrated the potential hazard of this practice (Castle and others, 2001) even with disease precautions and quarantine of the prairie dogs. Vaccination of captive ferrets against plague could reduce this risk. Ferrets intended for release into the wild could be immunized with F1-V antigen several times prior to release and reimmunized upon recapture, preferably within 6 months to 1 year postrelease. This might reduce mortality rates of ferrets during plague outbreaks. However, because black-footed ferrets are completely dependent on prairie dogs for their survival and prairie dogs are likewise highly susceptible to plague, the ultimate recovery of ferrets will require maintenance of stable prey populations and thus prevention of plague in prairie dogs.

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References Cited

Barnes, A.M., 1982, Surveillance and control of bubonic plague in the United States: Symposia of the Zoological Society of London, v. 50, p. 237–270.

Barnes, A.M., 1993, A review of plague and its relevance to prairie dog populations and the black-footed ferret, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 28–37.

Barnham, M., Thornton, T.J., and Lange, K., 1983, Nephritis caused by *Streptococcus zooepidemicus* (Lancefield Group C): Lancet, v. 1, no. 8331, p. 945–948.

Castle, K.T., Biggins, D., Carter, L.G., Chu, M., Innes, M., and Wimsatt, J., 2001, Susceptibility of the Siberian polecat to subcutaneous and oral *Yersinia pestis* exposure: Journal of Wildlife Diseases, v. 37, p. 746–754.

Divers, T.J., Timoney, J.F., Lewis, R.M., and Smith, C.A., 1992, Equine glomerulonephritis and renal failure associated with complexes of group-C streptococcal antigen and IgG antibody: Veterinary Immunology and Immunopathology, v. 32, p. 93–102.

Francis, A.J., Nimmo, G.R., Efstratiou, A., Galanis, V., and Nuttall, N., 1993, Investigation of milk-borne *Streptococcus* *zooepidemicus* infection associated with glomerulonephritis in Australia: Journal of Infection, v. 27, p. 317–323.

Hafner, D.J., Yensen, E., and Kirkland, G.L., Jr., 1998, North American rodents—status survey and conservation action plan: Gland, Switzerland, International Union for the Conservation of Nature and Natural Resources/Species Survival Commission Rodent Specialist Group, 171 p.

Heath, D.G., Anderson, G.W., Jr., Mauro, J.M., Welkos, S.L., Andrews, G.P., Adamovicz, J.J., and Friedlander, A.M., 1998, Protection against experimental bubonic and pneumonic plague by a recombinant capsular F1-V antigen fusion protein: Vaccine, v. 16, p. 1131–1137.

Pinto, S.W.L., Sesso, R., Vasconcelos, E., Watanabe, Y.J., and Pansute, A.M., 2001, Follow-up of patients with epidemic poststreptococcal glomerulonephritis: American Journal of Kidney Diseases, v. 38, p. 249–255.

Rocke, T.E., Mencher, J., Smith, S.R., Friedlander, A.M., Andrews, G.P., and Baeten, L.A., 2004, Recombinant F1-V fusion protein protects black-footed ferrets (*Mustela nigripes*) against virulent *Yersinia pestis* infection: Journal of Zoo and Wildlife Medicine, v. 35, p. 142–146.

Schiller, C.A., Wolff, M.J., Munson, L., and Montali, R.J., 1989, *Streptococcus zooepidemicus* infections of possible horsemeat source in red-bellied tamarins and Goeldi's monkeys: Journal of Zoo and Wildlife Medicine, v. 20, p. 322–327.

Shaw, M., Montali, R.J., and Bush, M., 1984, *Streptococcus zooepidemicus* in small carnivorous mammals fed uncooked horsemeat: Journal of Zoo Animal Medicine, v. 15, p. 161–164.

Williams, E.S., Mills, K., Kwiatkowski, D.R., Thorne, E.T., and Boerger-Fields, A., 1994, Plague in a black-footed ferret (*Mustela nigripes*): Journal of Wildlife Diseases, v. 30, p. 581–585.

Zar, J.H., 1999, Biostatistical analysis (4th ed.): Upper Saddle River, New Jersey, Prentice Hall, 929 p.

The Quest for a Safe and Effective Canine Distemper Virus Vaccine for Black-footed Ferrets

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Abstract

Canine distemper virus (CDV) causes a systemic disease that is highly virulent to mustelids and other carnivore (Order Carnivora) species and is found worldwide. Endemic canine distemper in wild and domestic carnivores in the United States has made reintroduction of endangered black-footed ferrets (*Mustela nigripes*) difficult in the absence of safe and effective CDV vaccines and vaccination practices. Toward this end, researchers have explored appropriate animal models and vaccine preparations in highly susceptible species. Published studies involving domestic ferrets (*M. putorius furo*) using Galaxy-D® and evaluating a recombinant canarypox-vectored vaccine for oral administration are reviewed. In addition, we present new findings in domestic and black-footed ferrets and Siberian polecats (*M. eversmannii*) that have extended our understanding of CDV in the black-footed ferret and other at-risk carnivore species. Original research presented here includes trials that determined an effective challenge dose (by route) of virulent CDV in domestic ferrets and Siberian polecats; the low likelihood of collateral vaccination with Galaxy-D; the adverse effect of modified-live virus boostering in black-footed ferrets receiving killed vaccine previously and the response of Siberian polecats receiving canarypox-vectored recombinant CDV vaccine (reCDV); the absence of an effect of reCDV vaccination on conception, pregnancy, and neonatal growth in Siberian polecats; and the apparent inefficacy of active reCDV vaccination during the period of passive immunity in young Siberian polecats. In the final section, we discuss emerging concerns and avenues for disease intervention that may present new opportunities to solve problems in vaccine safety, vaccine availability, field vaccine delivery, and other therapeutic modalities.

Keywords: black-footed ferret, canarypox, canine distemper, ferret, morbillivirus, oral vaccine, paramyxovirus, recombinant, Siberian polecat

Introduction

Canine distemper virus (CDV; family Paramyxoviridae, genus *Morbillivirus*) is a single-stranded, negative sense, 16-kilobase RNA virus encoding six genes (designated N, P, M, F, H, L) and eight protein products. The N gene has been used for diagnostic CDV identification (Wimsatt and others, 2001; Rzezutka and Mizak, 2002) while the M and P genes have been used in phylogenetic analyses (Barrett and others, 1993; Saliki and others, 2002) and subtype identification (Roelke-Parker and others, 1996; Carpenter and others, 1998; van de Bildt and others, 2002; Bronson and others, 2003), respectively. Phylogenetic analysis using other genes has repositioned CDV within the paramyxoviridae (Westover and Hughes, 2001). Vaccine developers have focused on hemagglutinin (HA) and fusion (F) gene product antigens, which appear to confer highly protective immunity when antibodies are successfully raised in response to vaccination.

Canine distemper virus is found worldwide. The hallmarks of CDV-induced disease are the result of primary host tissue tropisms for the cutaneous (maculopapular rash, erythema), respiratory (increased respiratory rate or labored respirations, dyspnea, cyanosis), gastrointestinal (diarrhea), and central and peripheral nervous systems. While respiratory and gastrointestinal manifestations of this disease can cause considerable morbidity and mortality, it is often the central nervous system manifestations that portend death during its clinical expression (Leisewitz and others, 2001). Nervous signs attributed to CDV include seizures, tremors, depression, and myoclonia (peripheral nervous signs). While some tissue tropism differences in CDV are expected, the Center for Veterinary Biologics (CVB; Veterinary Services, Animal and Plant Health Inspection Service, U.S. Department of Agriculture [USDA]) virulent challenge strain ultimately leads to neurological disease; nervous signs can also dominate in

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previously vaccinated mustelids that ultimately succumb to CDV infection (J. Wimsatt, unpub. data, 1996–98).

Canine distemper primarily affects carnivores (Order Carnivora), but may opportunistically infect other taxa (Appel and others, 1991; Svansson and others, 1993; Appel and Montali, 1994; Appel and Summers, 1995; Kennedy and others, 2000; Pollack, 2001; Noon and others, 2003). In terms of its risk to endangered carnivores, CDV is the most significant pathogenic virus known, and the black-footed ferret (*Mustela nigripes*) reintroduction program must address this ongoing threat to captive breeding and wild population stability (Williams and Thorne, 1996).

It is the general intent of this paper to accomplish two somewhat disparate goals. First, we chronicle what research on canine distemper virus prophylaxis in mustelids has revealed, the roles of various animal models and vaccine preparations in the quest, and where new discoveries could likely lead these pursuits in the future. Second, we present new findings of black-footed ferret responses to CDV vaccination and studies using CDV vaccines in surrogate animals to find a practical approach for CDV prophylaxis in susceptible *Mustela* species.

The Ecology of Canine Distemper Virus and the Risk It Presents to the Black-footed Ferret

Canine distemper virus is enzootic in urban and rural settings (Grinder and Krausman, 2001). Canine distemper virus becomes rapidly inactivated once in the environment (Fox and others, 1998) but is readily spread by aerosol, even under dry, hostile conditions (Williams and others, 1988, 1997). In the wild, transfer can occur at carnivore food (e.g., burrow entrances) and water sources. Wildlife epizootics may emerge as a consequence (Noon and others, 2003).

Traditionally, the primary reservoir and ultimate source of CDV outbreaks in the wild is assumed to be unvaccinated domestic dogs that infect wildlife with CDV during chance encounters. The potential role of wild carnivores (especially young) as primary reservoirs of CDV is difficult to discount (Guo and others, 1986; Gese and others, 1991, 1997; Williams and Thorne, 1996; Williams and others, 1997; Cypher and others, 1998; Grinder and Krausman, 2001; Arjo and others, 2003) since high CDV seroprevalence rates, suggestive of high levels of exposure, are found in several wild species (Guo and others, 1986; Gese and others, 1991, 1997; Williams and others, 1997; Cypher and others, 1998; Dunbar and others, 1998; Truyen and others, 1998; Grinder and Krausman, 2001; Ikeda and others, 2001). During a recent outbreak of CDV at an urban zoo, wild raccoons (*Procyon lotor*) were found to harbor a unique CDV variant (Lednicky and others, 2004), and they appeared to serve as a distinct reservoir. Most dogs are vaccinated for CDV (Greene and Appel, 1998); as a result, wild carnivores may be of greater infective potential to high-risk species, such as the black-footed ferret, than are domestic dogs. However, resident CDV in domestic dogs is under strong vaccine-induced selection pressure (Mochizuki and others, 1999; Hashimoto and others, 2001; Lednicky and others, 2004) and thus cannot be discounted as an emergent source in the future.

One area of growing relevance to captive and exotic carnivores is the possibility of CDV persistence and later viral shedding (elaboration and release of virus by renewed replication from the host at a later date) after the primary infection has subsided. This issue is of great concern where modified-live virus (MLV) vaccines are used in nontarget species.

Persistence of morbillivirus infections has led to such diseases as subsclerosing panencephalitis in humans (Dyken, 2001; Garg, 2002; Schneider-Schaulies and others, 2003), Paget’s disease (Cartwright and others, 1993; Fraser, 1997; Mee and others, 1998; Friedrichs and others, 2002; Hoyland and others, 2003), and canine orthopedic conditions (Mee and others, 1993; Harrus and others, 2002). Autoimmune-mediated demyelination associated with measles or CDV infection has been studied in relation to its possible association with multiple sclerosis (Anonymous, 1978; Appel and others, 1981; Cook and others, 1986; De Keyser and others, 2001; Hernan and others, 2001). A link between infectious obesity and CDV has been proposed as well (Dhurandhar, 2001; Verlaeten and others, 2001).

Recently, evidence of CDV persistence has been documented in domestic dogs in which selected strains of the virus survived without detection by the host immune system (Lincoln and others, 1971; Povey, 1986; Leisewitz and others, 2001). A major requirement for chronically persistent CDV infection involves the selection of a cell-associated strain with limited capability for antigen presentation (Vandevelde and Zurbriggen, 1995) and conferring only limited antibody diversity (Rima and others, 1987); this latter strain differs in its pathogenesis from more virulent forms causing acute disease (Vandevelde and others, 1980). One key site of CDV persistence may be dendritic cells, reflecting a change in CDV cell tropism (Wunschmann and others, 2000). The condition “old dog encephalitis” is one presentation of chronic CDV infection (Lincoln and others, 1971; Hall and others, 1979; Tobler and Imagawa, 1984; Evans and others, 1991; Axthelm and Krakowka, 1998). Moreover, a tropism for epithelial cells (in addition to the typical tropism for macrophages) in culture suggests that persistent strains behave more akin to vaccine strains (Evans and others, 1991). A recent case report highlighted the risk of CDV persistence from vaccine strains when a red panda (*Ailurus fulgens*) vaccinated 3 years earlier with a commercial MLV CDV vaccine developed progressive CDV-induced neurological disease and subsequently died (Bronson and others, 2003). Gene typing (P gene) demonstrated that the offending CDV isolate was actually the original vaccine strain. Another recent paper suggested that incomplete CDV expression of fusion (F) protein may facilitate persistent viral infection; likewise, hemagglutinin (HA) heterogeneity of new emerging strains could lead to more widespread CDV persistence if F protein immunity becomes the primary source of protection following vaccination (Meertens and others, 2003).

Animal Models for Testing CDV Vaccines Destined for the Black-footed Ferret

Historically, guidelines for vaccinating free-ranging and captive wild carnivores were derived from those used for vaccines in domestic dogs, mink (Hagen and others, 1970), and domestic ferrets (*M. putorius furo*) (Hagen and others, 1970; Farrell and others, 1971). Interestingly, while domestic dogs are commonly vaccinated, they are not among the most CDV-susceptible carnivore species. One study estimated that up to 70 percent of urban dogs that were exposed to natural CDV infection never developed overt disease signs although they seroconverted, suggesting occult infection (Rockborn, 1957). Likewise, experience has shown that vaccines developed for high efficacy in dogs (and also sometimes used safely in some wild canids) may be too virulent for more susceptible species (Fox and others, 1998) such as red pandas (Bush and others, 1976; Itakura and others, 1979; Montali and others, 1983; Appel and Summers, 1995), gray foxes (*Urocyon cinereoargenteus*) (Halbrooks and others, 1981), and selected *Mustela* species (Carpenter and others, 1976; Montali and others, 1983, 1994; Sutherland-Smith and others, 1997). Canine cell line origin passaged vaccines were quickly realized to be pathogenic to domestic ferrets, commonly vaccinated as pets against CDV (Fox and others, 1998). Early MLV CDV vaccines intended for ferrets utilized primary chick embryo passage. These procedures were expensive, and assuring product uniformity was an ongoing concern (Fox and others, 1998).

An immune deficiency in black-footed ferrets that may be of prime importance in explaining the unique, extreme susceptibility of this species to CDV and other infectious diseases is the diminished production of the proimmune cytokine interleukin-6 (Stoskopf-Kennedy and others, 1997). In contrast, Siberian polecats (*M. eversmannii*) appear to produce greater amounts of interleukin-6 (S. Wisely, oral commun., 2004). Homozygosity among Wyoming black-footed ferrets is recognized from genetic comparisons to historical populations from Kansas and to Siberian polecats (Wisely and others, 2002); this limited diversity may have contributed to the unique susceptibility of black-footed ferrets to natural and vaccine strains of CDV. Further investigations will reveal whether other highly susceptible species exhibit the same predisposition to diminished interleukin-6 production. Other cytokines need to be explored in this light as well (Bencsik and others, 1996; Grone and others, 2002).

A recent refinement in the production of one widely used CDV vaccine strain involved serial passage of the virus on an immortal primate Vero cell line (rather than chick embryo) and a more controlled process of vaccine attenuation. These procedures appear to improve product reliability, but highly susceptible species still succumb to vaccine-induced viral disease (Sutherland-Smith and others, 1997).

The characterization of appropriate models for the study of CDV vaccines in susceptible species has been a high priority. Based on taxonomy, domestic ferrets appeared to provide a close model for interpreting the likely CDV responses of black-footed ferrets as compared with other carnivores; more closely related Siberian polecats (O'Brien and others, 1989) and black-footed ferret × polecat hybrids helped to further define the likely impact and efficacy of existing vaccine strategies destined for the black-footed ferret (Williams and others, 1996). Recently, surplus black-footed ferrets have sometimes been available for CDV vaccine studies (J. Kreeger, oral commun., 2004), but definitive challenge studies may still rely heavily on other mustelid models.

Vaccines: the Past, Present, and Future

Traditionally, killed virus (KV) vaccines were reserved for species and situations where MLV vaccines were considered unsafe. Potential disadvantages of KV vaccines include: unreliable inactivation; short-lived immunity (in addition, adjuvants that may cause some side effects may be required); the need for high antigenic doses (possible side effects if redosed); variable protection in poor responders; and finally, the induction of humoral (antibody production) rather than cell-mediated (i.e., T cell-mediated cellular) immunity (Schultz and Zuba, 2003). Thus, KV vaccines may not protect against overwhelming exposures to wild-type CDV; protection in such instances likely requires both robust humoral and cell-mediated immune responses. A nonadjuvanted KV vaccine was produced for use in highly susceptible species such as the black-footed ferret and red panda by Dr. Max Appel, of the Baker Institute at Cornell University; this vaccine was provided until a more favorable vaccination strategy became available.

Commercial CDV vaccines are primarily modified-live products incorporating carefully selected wild strains that respond favorably to serial passage and graded attenuation. Of these, the Onderstepoort strain has been most extensively used for vaccination in the domestic ferret and exotic carnivores in zoological collections, first as the chick-embryo product Fromm-D (Solvay Co., Mendota Heights, Minn.; no longer produced) and later as the primate Vero cell line attenuated vaccine, Galaxy-D® (Schering-Plough Animal Health, Inc., Union, N.J.). As a rule, modified-live products do not supply sufficient antigenic load to confer immunity unless active infection is engendered by vaccination (Schultz and Zuba, 2003). A recent study on the efficacy of Galaxy-D in domestic ferrets demonstrated, by polymerase chain reaction (PCR) amplification, the presence of CDV vaccine virus in the blood

5 days following the first of two inoculations. A primary vaccination series led to protective immunity as defined by virulent strain challenge (Wimsatt and others, 2001). Modified-live CDV vaccines have been shown to provide substantial and long-lived immunity following a primary vaccination series that invokes both cell-mediated and humoral immunity in dogs and domestic ferrets (Gorham, 1966, 1999). In the past, Fervac-D® (United Vaccines, Inc., Madison, Wis.) and other modified-live CDV vaccines (Fromm-D and Galaxy-D) routinely used in domestic ferrets were tested in surrogate species and were found unsuitable for black-footed ferrets. Either primary (CDV-induced) or secondary immunosuppression-related disease ensued when black-footed ferrets and black-footed ferret hybrids were vaccinated with these formulations (E. Williams, oral commun., 1995). Lymphocyte apoptosis accompanies CDV infection leading to its immunosuppressive effects (Moro and others, 2003a,b). As with natural infection, the immunosuppressive fallout of CDV infection from modified-live vaccination can lead to significant secondary morbidity and mortality in stressed or particularly susceptible individuals. The closely related measles and CDV viruses directly inactivate lymphocytes by virus-dependent and independent means (Krakowka, 1982) whereas more “adapted” strains do not inhibit lymphocyte proliferation (Schultz, 1976; Schlender and others, 1996) or T cell-mediated cytotoxicity (Tipold and others, 1999), and lead to the elaboration of immune-modulatory substances (Krakowka and others, 1987; Tipold and others, 1999).

Our interest in modified-live CDV vaccination in the black-footed ferret arose in exploring the possibility that a reliable, less virulent, modified-live vaccine might be used to booster black-footed ferrets that had been vaccinated previously with a KV vaccine. A modified-live CDV booster would be expected to last for the reproductive life of the animal, thus obviating the need for vaccination in the wild after reintroduction. Experimental KV vaccine (inactivated Onderstepoort strain) was widely used by zoos to protect high-risk species such as lesser pandas and black-footed ferrets (R. Montali, oral commun., 1996), but a vaccinated cohort had never been extensively challenged under controlled conditions to determine efficacy because of the scarcity and inherent value of these species. Use of a CDV modified-live booster following repeated KV vaccination served as a mild challenge. Boostering efficacy was further tested by subsequent virulent strain challenge. Based on experience gleaned from studies on surrogate species and hybrids with various candidate vaccines, current vaccine trials now focus primarily on safer subunit vaccines for genetically “bottlenecked” or exquisitely susceptible species.

More recently, the advent of vectored vaccines employing a wide range of different vectors and supplying antigens for many diseases affecting many species (Tartaglia and others, 1990, 1992, 1993; Paoletti and others, 1993, 1994, 1995; Taylor and others, 1994; Pincus and others, 1995) has fostered new optimism about the potential to find a safe and effective CDV vaccine for use in highly susceptible species.

Recent Studies Guiding Use of CDV Vaccine in Mustelids

All animals undergoing vaccine and challenge trials described below were housed in a biosafety level-2 room in modified rabbit cages and fed a high quality cat (Siberian polecats or domestic ferrets) or mink (black-footed ferret) chow; water was provided free choice. Animals were randomly assigned to treatment groups unless otherwise specified and grouped in cage racks by treatment. All animals were supplied with 40.6-cm (10.2-cm diameter) PVC hide tubes with fixed end caps. Animals were anesthetized without restraint by placing a second end cap with an inhalant anesthetic delivery port over the opposite end while the animal was inside.

Anesthesia was induced using 5 percent isoflurane in 3 L/min oxygen. After approximately 2 minutes, the animal was transferred from the PVC chamber to a face mask, and anesthesia was maintained at 1–2 percent isoflurane in 1.5 L/min oxygen. Care was taken to anesthetize the controls before the vaccinates in all cases. Blood samples (1 mL) were collected from the cranial vena cava or from an external jugular vein into serum tubes, and serum was frozen until assayed. Under anesthesia, vaccination was accomplished by subcutaneous injection (Galaxy-D, following the manufacturer’s instructions, and canarypox-vectored recombinant canine distemper virus [reCDV] vaccine), or by the oral route (reCDV), spraying the reconstituted vaccine in the back of the mouth.

Serology and Challenge Strain Dose Validations

An adapted standard serum microneutralization test was used to assess CDV titers (Appel and Robson, 1973). All virulent CDV challenge studies employed the CVB USDA Snyder Hill virulent challenge strain (Lot # 90-18). This same strain is used for vaccine challenge studies required for USDA licensing of commercial CDV vaccines. Dose selection for these studies was validated as described below.

Initial challenge dose-response studies using six domestic ferrets per group and five dose groups (J. Wimsatt, unpub. data, 1996) established a minimal 100 percent lethal intraperitoneal dose of CVB Lot # 90-18 challenge strain ferret spleen suspension in domestic ferrets as a dilution of 1:1,000 (pH 7.0, delivered in 1 mL total volume). Thus, for all subsequent challenge studies, regardless of the *Mustela* species tested, a 1-mL volume of challenge strain diluted to 1:250 in phosphate buffered saline (same pH and total volume) was used. This final lethal dose selected for challenge studies was confirmed in four Siberian polecats (J. Wimsatt, unpub. data, 1996) and was also found to be 100 percent effective (lethal) when used in challenge controls in subsequent studies. Later investigations extended these initial determinations to suggest that combined oral/intranasal instillation yielded the same results as intraperitoneal administration in Siberian polecats (J. Wimsatt, unpub. data, 1997) and domestic ferrets (Wimsatt and others, 2001). The only exception was that CDV-induced skin erythema or maculopapular rash usually occurred first at the site of challenge strain inoculation.

Challenge studies still remain the best available means to test vaccine efficacy. The significance of different routes of challenge, like those influencing vaccination, may be of considerable importance and requires careful study (Schultz and Zuba, 2003). While intracerebral and intraperitoneal challenge are commonly used, mucosal (intranasal/oral) challenge more closely mimics natural infection. Mucosal immunity is often considered the first line of defense against infectious agents (Ogra and others, 1980). In our studies, using survival as the endpoint, the intraperitoneal and oral/intranasal routes yielded similar results. This is of interest since CDV has a tropism for mucosal tissue (Jozwik and Frymus, 2002), and mucosal presentation to dendritic cells may stimulate cell-toxic lymphocytes (Etchart and others, 2001) early in the disease pathogenesis. Likewise, active CDV mucosal immunization may minimize disease-induced immunosuppression (Liashenko and others, 1999) or bypass maternal passive immunity (Fischer and others, 2002), leading to qualitatively different outcomes during challenge and vaccination. During challenge, such differences were not evident.

Modified-live Vaccine Studies in Domestic Ferrets

A chick embryo origin product (Fromm-D) using an attenuated Onderstepoort strain was found to be safe and effective when tested in black-footed ferret × Siberian polecat hybrids (Williams and others, 1996) and domestic ferrets (Fox and others, 1998). Galaxy-D was tested in male domestic ferrets vaccinated and challenged as described previously (Wimsatt and others, 2001). Briefly, eight randomly selected CDV-seronegative male domestic ferrets (Marshall Farms, Rose, N.Y.) were subcutaneously vaccinated twice 4 weeks apart with Galaxy-D according to the manufacturer's instructions. Eight control animals received saline injections. Challenge followed 21 days after the last vaccination (Wimsatt and others, 2001).

Virulent virus challenge produced 100 percent mortality in the controls, with prolonged presence of virus nucleoprotein in the blood detected by CDV-specific nucleoprotein reverse transcriptase PCR (RT-PCR). All Galaxy-D vaccinates (*n* = 8) survived following a primary two vaccine series although one first-time and two second-time vaccinates expressed viral nucleoprotein in their blood following challenge (Wimsatt and others, 2001). After active infection, this MLV vaccine induced a robust immune response protective against lethal CDV challenge, indicating that domestic ferrets responded with protective adaptive immunity to this same CDV strain, originally packaged in the avian embryo passaged Fromm-D vaccine.

Domestic Ferret Collateral Vaccination of Cage Mates

In a second study, randomly selected pair-housed male CDV-seronegative domestic ferrets were subcutaneously vaccinated with a single dose of Galaxy-D. Blood sampling for serology and challenge were performed as indicated in fig. 1. Unvaccinated CDV-naïve cage mates were blood-sampled for seroconversion to assess for collateral vaccination.

None of the six male co-housed domestic ferrets seroconverted in response to a single Galaxy-D delivered to their (CDV-naïve) cage mate up to 25 days after vaccination. All vaccinated ferrets (six of six) survived challenge following the single Galaxy-D dose. Serology values for unvaccinated cage mates, vaccinates, and unvaccinated controls are shown in fig. 2; titers for unvaccinated cage mates housed contemporaneously with Galaxy-D vaccinates remained low and indistinguishable from those of seronegative controls (fig. 2), suggesting that if primary vaccine shedding or contamination following vaccination occurred, it was insufficient to produce a MLV-induced immune response in the CDV-naïve cage mates.

Subcutaneous vaccination of CDV-naïve domestic ferrets with Galaxy-D did not appear to present a sufficient antigenic dose for collateral vaccination of co-housed cage mates and thus did not lead to seroconversion. This is not surprising since modified-live virus load is typically too low to induce an immune response in the absence of a host infection (i.e., host infection replicates more virus, thus increasing its antigenic load) caused by the vaccine strain (Schultz and Zuba, 2003). However, the timeframe was not sufficient to conclude that shedding of the Galaxy-D CDV virus from vaccinates would not have occurred eventually from virus replication in the host.

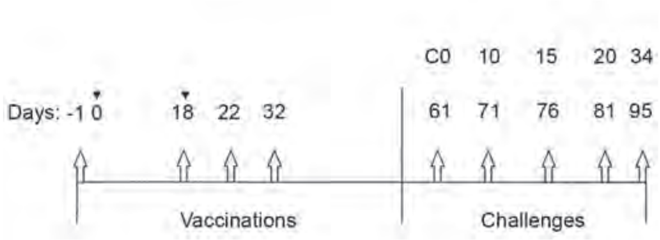

Figure 1. Timeline for the black-footed ferret (*Mustela nigripes*) Galaxy-D booster and virulent canine distemper virus challenge study. Seronegative domestic ferrets (*M. putorius furo*) in the same room served as challenge strain controls, and another cohort of pair-housed domestic ferrets had one member of the pair randomly selected for Galaxy-D vaccination at the same time; vaccinates were later challenged with the others while the unvaccinated member of the pair was removed just prior to challenge. Triangles indicate days of vaccination. Arrows indicate days when blood samples were drawn.

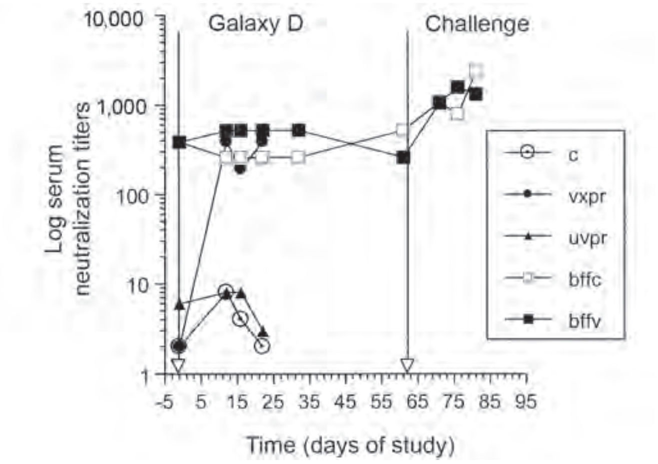

Figure 2. Serum neutralization titers for domestic ferret (*Mustela putorius furo*) controls (c), vaccinated domestic ferrets (vxpr), pair-housed unvaccinated domestic ferrets (uvpr), previously vaccinated older black-footed ferrets (*M. nigripes*) receiving Galaxy-D boostering prior to challenge (bffv), and previously vaccinated older black-footed ferrets challenged with canine distemper virus (bffc). Controls and unvaccinated pair-housed domestic ferrets did not exhibit significant titer increases. Black-footed ferrets started with high median titers from previous vaccinations, but boostering with Galaxy-D had no significant effect on their titers. Challenge caused elevated titers in the survivors.

Black-footed Ferrets

Nonreproductive, older (6–8 years), mixed-sex black-footed ferrets (culled from the breeding program) that had previously received one or more experimental KV vaccinations (an Onderstepoort strain-origin experimental vaccine produced by M. Appel, Baker Institute, Cornell University) were randomly assigned to one of two treatment groups after being matched for CDV serum neutralization titer across groups prior to study. At the beginning of the study, the first group (n = 8) received a single dose of Galaxy-D subcutaneously while the second group (n = 7) served as controls. Surviving vaccinates (n = 6) and controls (n = 5) were challenged 61 days later. The timeline for the experiment is shown in fig. 1. The primary endpoint of interest was survival although necropsies were performed to determine pathological changes following challenge as well as the cause of death.

Serum neutralization titers in surviving black-footed ferrets revaccinated with Galaxy-D and previously vaccinated (with the M. Appel killed CDV vaccine) black-footed ferret controls were comparable to those observed in newly vaccinated domestic ferrets receiving Galaxy-D for the first time. As expected, these titers contrasted sharply with those of unvaccinated seronegative domestic ferret controls (fig. 2). Prior to challenge, one black-footed ferret with a titer of 1:8 from prior vaccination succumbed (one of eight) to vaccine strain CDV 15 days after vaccination, and another died from a secondary infection, likely related to CDV-induced immunosuppression (*Clostridium* sp. was isolated from this case of vascular sepsis). In addition, a control black-footed ferret (unvaccinated during the present trial) succumbed to CDV (one of seven; it succumbed 32 days after vaccine delivery and had an initial titer of 1:64) although it was housed in a separate rack of cages adjacent to the black-footed ferret vaccinates. Following challenge, three of six vaccinates died, one 17 days after challenge (1:512). Of black-footed ferret controls, when they were finally challenged, one died 11 days later, and another died in response to a secondary infection (*Enterobacter faecalis*-induced sepsis). All black-footed ferret challenge survivors developed elevated CDV titers.

Previously, CDV-naïve black-footed ferrets were shown to be highly susceptible to the development of canine distemper even when the virus (canine passaged) was supplied by vaccination as a modified-live CDV strain (Carpenter and others, 1976). The presence of high titers from the KV vaccine appeared protective for black-footed ferrets exposed to live attenuated CDV in vaccine (Galaxy-D) or to the challenge strain; nevertheless, high titers alone were not always indicative of protection, as illustrated by one animal with a high titer (1:512) that still succumbed to CDV. From this series, MLV boostering of black-footed ferrets with high circulating CDV titers was of marginal value, most likely due to the blocking effect of these antibodies on the vaccine strain. There is no evidence that cell-mediated immunity was enhanced from boostering. Even so, overall, titers above 1:64 in this series appeared to confer protection against CDV challenge. Perhaps more important was the observation that protection against CDV did not necessarily ameliorate the likelihood of immunosuppression and death from secondary invaders. Finally, of those succumbing to CDV, the precipitous onset of neurological signs, without other prodromal signs, was the hallmark of disease development in prior vaccinates. This has been explained as a persistence of F protein-directed immunity with waning HA protection and is qualitatively similar to the outcome observed when CDV-infected vaccinates encounter novel CDV strains where HA antigenicity has shifted (Stern and others, 1995).

Canarypox-vectored Vaccination and the Potential for Oral Vaccine Delivery

A dose-response study was performed to define the minimum protective dose and chronicle possible side effects of an experimental canarypox-vectored recombinant CDV vaccine (reCDV) in Siberian polecats, as described in detail elsewhere (Wimsatt and others, 2003). Briefly, subcutaneous dose groups received $10^{5.5}$, $10^{5.0}$, or $10^{4.5}$ plaque-forming units (PFU, a measure of vector and therefore vaccine concentration), and oral dose groups received $10^{8.0}$ and $10^{5.5}$ PFU. The timeline used for vaccination, blood sampling, and challenge is shown in fig. 3; challenge was performed 61 days after the

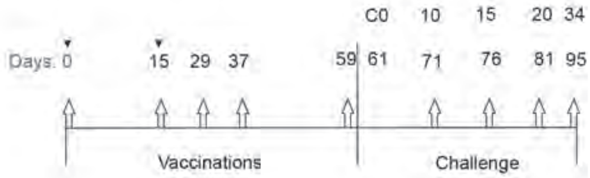

Figure 3. Timeline for canarypox-vectored recombinant canine distemper virus vaccine (reCDV) trials in Siberian polecats (*Mustela eversmannii*) and in the reCDV-Galaxy-D boostering study where the same timeline was used except that Galaxy-D was substituted for the second reCDV vaccination. Triangles indicate days of vaccination. Arrows indicate days when blood samples were drawn.

first vaccination. For standardization purposes, only vaccine expressing >95 percent expression-capable canarypox vaccine vector was used. Outcomes included CDV-associated clinical sign development, survival of virulent challenge postvaccination, and antibody development; only the latter two outcomes will be recounted here.

As previously reported, oral reCDV vaccination of Siberian polecats with $10^{8.0}$ PFU vaccine was protective for five of six vaccinates, or 83.3 percent effective in protecting Siberian polecats against lethal CDV challenge (Wimsatt and others, 2003). A difference in survival following challenge was noted in groups receiving the same vaccine dose ($10^{5.5}$ PFU) by different routes (oral vaccine, none of six survived challenge; subcutaneous vaccine, three of six survived) indicating that the parenteral route was superior to oral delivery. The difference in challenge survival between the $10^{5.5}$ PFU (three of six survived) and $10^{5.0}$ PFU (three of five survived) subcutaneous dose groups was not significant, suggesting the minimal protective CDV PFU dose is higher than $10^{5.5}$.

A Kaplan-Meier survival analysis was performed with dose and route of reCDV administration as predictors (fig. 4) (Wimsatt and others, 2003). Protective titers in response to reCDV were typically lower than those measured following vaccination with Galaxy-D in naïve animals; higher relative titers in response to reCDV were associated with greater protective value of the vaccine, and generally predictive of vaccine efficacy overall, as was the case for the modified-live vaccine. Even so, some challenge survivors that received reCDV had titers low enough that they would have been predicted to succumb to the challenge if modified-live vaccine protective titers were used as a guideline (e.g., 1:50–100; see fig. 5). It seems plausible that the protective titer differential between reCDV and modified-live vaccines in challenge survivors reveals that cell-mediated immunity conferred by the reCDV vaccine is a major aspect of its protective effect.

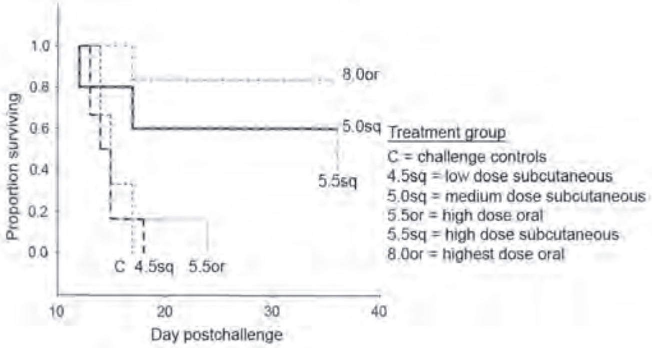

Figure 4. A survival curve is shown for canarypox-vectored recombinant canine distemper virus vaccine trials with Siberian polecats (*Mustela eversmannii*). Animals receiving two $10^{8.0}$ PFU vaccinations orally (8.0or) survived. Those receiving lower subcutaneous doses (e.g., 5.0sq) had lower survival as did those receiving lower oral doses (e.g., 5.5or), which fared even worse. (From Wimsatt and others, 2003. Reprinted with permission of the *Journal of Zoo and Wildlife Medicine*.)

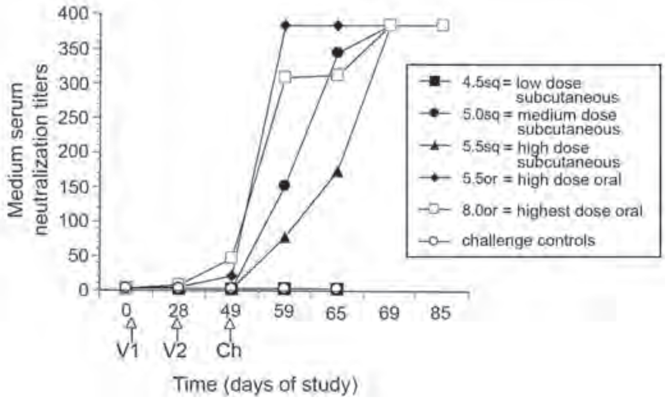

Figure 5. Serology results from the canarypox-vectored recombinant canine distemper virus (CDV) vaccine dose-response study where varied doses were administered subcutaneously or orally under isoflurane anesthesia. These results indicated that survivors mounted CDV serum neutralization titers above those of nonsurvivors. An exception was noted in the case of the oral $10^{5.5}$ group, where nonsurvivors mounted elevated titers, but these titers were insufficient for protection against challenge. Thus, a cell-mediated component of immunity, mounted at higher protective vaccine doses, must be important for vaccine efficacy with vectored subunit vaccines against CDV. V1 = first vaccination, V2 = second vaccination, Ch = challenge. (Adapted from Wimsatt and others, 2003. Reprinted with permission of the *Journal of Zoo and Wildlife Medicine*.)

Starting in the early 1990s, interest was developing among black-footed ferret conservationists for the identification of a safe and effective CDV vaccine to use in this endangered species. The potential to safeguard the black-footed ferret using a canarypox-vectored subunit vaccine led to a series of studies in Siberian polecats with the ultimate goal of applying this vaccine to the black-footed ferret; this work became a major focus starting in 1996. At the same time, it was recognized that this work could serve as a guide for other highly CDV-susceptible species. This vectored vaccine type, sometimes referred to as a type III recombinant vaccine (Van Kampen, 2001), used a canarypox vector to infect local (at the site of delivery) host cells, which then present HA and F antigens to T cells and macrophages, initiating cell-mediated and humoral responses (Schultz and Zuba, 2003). The canarypox vector was chosen because pox viruses do not use cell receptors for cell uptake during cellular endocytosis, the avian virus is avirulent at mammalian body temperatures, the pox genome is large enough to allow sizable vaccine-related gene substitutions, and pox vectors potentially reduce the risk of host genomic splicing (Tartaglia and others, 1992, 1993; Perkus and others, 1995a,b; Adams and others, 1997). Optimal recombinant vaccines are constructed to obtain high gene expression rates in host cells. Ideally, the immune system recognizes these cells and presents them to the humoral and cell-mediated arms of the immune system to develop a broad immune response with protective attributes somewhere between those of a modified-live vaccine and a KV vaccine (Schultz and Zuba, 2003). Advantages of this approach are that (1) no intact infectious agent is used, (2) pox virus products are more durable than modified-live CDV, and (3) adjuvants are not required. Vaccinated domestic cats (*Felis silvestris*) (Macy and Couto, 2001) appear to be at risk of developing injection site-associated sarcomas; this issue has also been raised with domestic ferrets, which appear at lower risk with recombinant vaccines (Merial Technical Services, oral commun., 2000). Another concern seen in domestic ferrets following repeated vaccination with approved modified-live products has been the increased risk of anaphylaxis (Fox and others, 1998). In one study surveying the risk of side-effects of vaccination in domestic ferrets, adverse reactions were reported approximately 5 percent of the time, particularly in older, previously vaccinated ferrets (Greenacre, 2003). This appears to be rarer with some products than others (Fox and others, 1998) and may be less likely with vectored vaccines although they have not been evaluated long enough to answer this question conclusively at this time. Repeated vaccination increased glomerular immune-complex deposition in mink receiving a multivalent vaccine that included CDV; unfortunately, the potential risk of glomerular disease was not studied (Newman and others, 2002). Recent anecdotal reports suggest that even the commercially available vectored CDV vaccine (PureVax® Ferret Distemper Vaccine; Merial, Inc., Athens, Ga.) is not without some risk in black-footed ferrets. Recently, several deaths in black-footed ferrets have been linked to its use in zoos (D. Garelle, oral commun., 2004).

Another important objective was to determine the efficacy of reCDV vaccine when delivered orally, so it could ultimately be used for wild black-footed ferrets in baits. Raboral V-RG® (Merial, Inc., Athens, Ga.), a vaccinia-vectored rabies subunit vaccine had been successfully packaged and broadcasted in baits to curtail fulminant rabies outbreaks in several wild carnivore populations (Fearneyhough and others, 1998; Hanlon and others, 1998; Olson and Werner, 1999). As demonstrated in domestic ferrets, vaccinia likely represents a better vector for oral administration than canarypox based on vaccination and challenge by enteric instillation (Welter and others, 1999). However, the risk of human infection when encountering the vaccinia vector remains of potential concern, particularly for immunocompromised individuals; a vectored-vaccine, bait-induced vaccinia infection was documented in a pet owner when she tried to remove a bait from her dog's mouth and was bitten in the process (Rupprecht and others, 2001). The appearance of a vaccinia strain from Brazil pathogenic to cattle and humans (Palca, 2005) may ignite a debate about the persistence of this virus, or of genetic constructs of this virus when used as a vector in the future.

Vaccination Effect on Humoral Immunity

In this study, pokeweed blastogenesis (pokeweed is a nonspecific B lymphocyte mitogen) was performed on blood samples from Siberian polecats collected immediately prior to and 14 days after a single reCDV vaccination ($10^{5.5}$ PFU) and coincidentally from unvaccinated saline control polecats.

Changes in blastogenesis responses of B lymphocytes in primary culture between vaccinates and controls were not statistically different (fig. 6). Hence, reCDV vaccination did not appear to cause significant suppression of B cell lines (immunosuppression) expected during sequelae of CDV modified-live vaccination and natural CDV infection.

In this study, we hypothesized that the immunosuppression associated with modified-live vaccination would not occur when using vectored CDV vaccines, a major

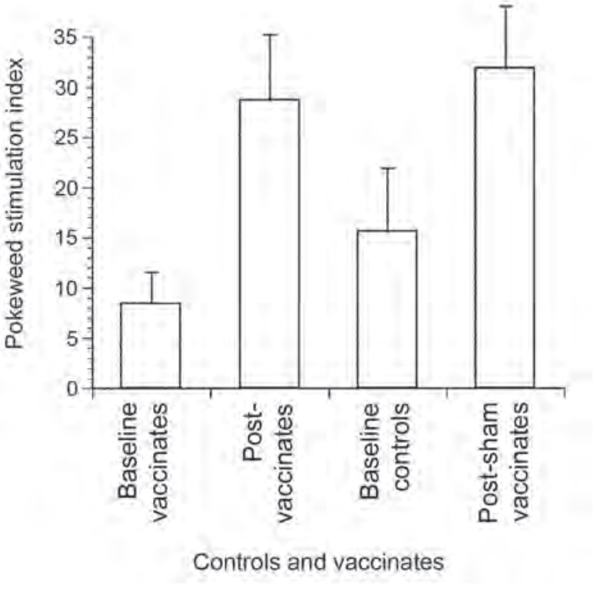

Figure 6. Pokeweed blastogenesis was performed on two samples of peripheral lymphocytes before and 14 days after canarypox-vectored recombinant canine distemper virus (reCDV) vaccination or saline control injections. The change in lymphocyte blastogenesis between controls and vaccinates was not significantly different and suggests that reCDV was not immunosuppressive as compared to live CDV exposure or modified-live virus vaccination.

advantage of the latter type. These results confirmed that the reCDV vaccine did not appear to cause a blunted B lymphocyte blastogenic response to pokeweed mitogen, typical of immunosuppression seen with modified-live CDV vaccines.

MLV Vaccine Boostering Following Vectored Vaccine

Onderstepoort strain origin genes for F and HA were used during construction of the reCDV vaccine and are expressed in Galaxy-D. To assess the potential for interference or synergy expected from use of reCDV followed by modified-live (Galaxy-D) vaccination, Siberian polecats that received a single reCDV dose ($10^{5.5}$ PFU) were subsequently boostered with Galaxy-D subcutaneously. These animals were challenged 61 days later. The timeline employed for blood sampling, vaccination, and challenge is depicted in fig. 3.

Five of five mixed sex Siberian polecats that received a single reCDV dose boostered with Galaxy-D survived challenge whereas six of six seronegative challenged controls succumbed.

This study in Siberian polecats showed that a single reCDV vaccination using the F and HA proteins from the Onderstepoort strain did not interfere with a single Galaxy-D vaccination that followed, in effect using the same antigens from this strain in both cases; likewise, during the challenge that followed, this combination provided 100 percent survival, and, in our hands, provided protection equivalent to that of a single Galaxy-D vaccination in domestic ferrets, as mentioned previously. The use of a MLV vaccine to booster the commercial reCDV vaccine (PureVax) is of interest to domestic ferret owners, and this practice has been shown to be effective in pet ferrets when using the currently USDA approved MLV (Fervac-D) vaccine (Merial Technical Services, oral commun., 2001). The production of low (blocking) titers and immune priming conferred by recombinant vectored vaccines may make them ideal candidates for MLV boostering that is expected to confer long-term immunity.

While not specifically tested, modified-live CDV boostering in black-footed ferrets suggests that modified-live vaccination following limited reCDV vaccination may be quite risky. Studies are in progress to establish the duration of titered immunity expected in black-footed ferrets over time following a primary two-vaccination series with PureVax (J. Kreeger, oral commun., 2004). Some investigators believe that three primary vaccinations will be warranted to provide a longer duration of immunity and higher protective titers (R. Montali, oral commun., 2003). Whether boostering with Galaxy-D or another relatively safe modified-live vaccine following some type of primary recombinant vaccination in black-footed ferrets will ever be worth the risk remains unclear. One important aspect of modified-live vaccination remains attractive; that is, the likely provision of life-long immunity in modified-live vaccinates. Immunity following a primary modified-live vaccination series with chick embryo attenuation was protective against lethal challenge at 6 years of age in mink and domestic ferrets (Burger and Gorham, 1964), and 5.5 years after similar vaccination in another domestic ferret study (Cabasso and Cox, 1953); this same result was reported in dogs 6.5 years after vaccination (L. Carmichael, personal commun., 1997, as reported by Gorham, 1999, p. 559). If repeated recombinant vectored vaccine vaccination does not confer life-long immunity, a trial to determine if MLV boostering following a full reCDV primary series may be warranted in black-footed ferrets destined for release, since it is highly unlikely they can be caught again for revaccination once in the wild. Alternatively, an effective oral baiting program with recombinant vaccine may be developed.

Vectored Vaccine Safety During Pregnancy

The timeline for vaccination, blood sampling, and challenge for evaluation of vectored vaccine safety in pregnant Siberian polecat females is shown in fig. 7 (upper timeline). Twelve treatment-randomized, unvaccinated Siberian polecat jills were compared to 12 reCDV vaccinates. Vaccination of CDV-naïve, reproductively intact polecat jills with a moderate reCDV dose ($10^{5.5}$ PFU subcutaneously) immediately prior to conception was followed by a second vaccine dose during the last 10 days of pregnancy.

Initial vectored vaccination had no significant effect on conception rates. Following a second vaccination at 29 days of gestation, birth outcomes such as litter size and kit rate of weight gain (measured from 17 to 35 days of age) were not significantly different from those in unvaccinated controls.

Canine distemper virus has been demonstrated to be capable of crossing the placental barrier of infected pregnant bitches and infecting their unborn puppies (Krakowka and others, 1974, 1977). Most reproductive-age bitches are either

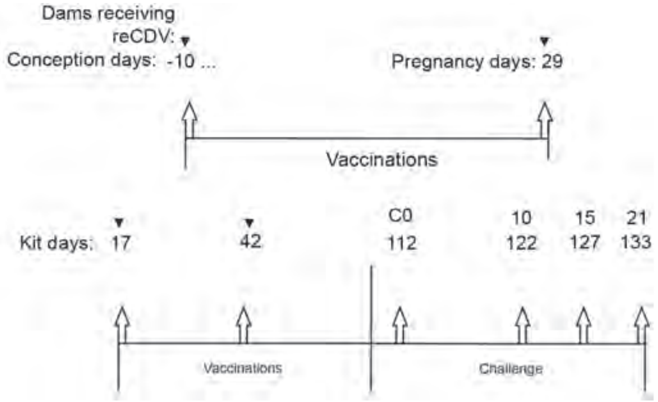

Figure 7. Timeline for the canarypox-vectored recombinant canine distemper virus (reCDV) immunization of Siberian polecat (*Mustela eversmannii*) dams to assess conception and pregnancy safety. Also shown is the timeline for vaccination of their kits in the passive immunity study. Triangles indicate days of vaccination. Arrows indicate days when blood samples were drawn.

vaccinated or exposed to CDV prior to pregnancy, conferring immunity; thus, it is likely that the potential for naïve dams of wild species or domestic canids to pass CDV transplacentally is underestimated (Krakowka and others, 1974), and the potential impact of CDV on reduced fecundity has not been well characterized in wild carnivores. Gorham (1999) conducted studies exploring the potential ill effects of vaccination before conception and during pregnancy employing a modified-live vaccine in mustelids. In those studies, modified-live vaccination influenced neither litter size nor apparent fertility; these results are similar to ours employing reCDV and suggest that high virus loads may be required to see transplacental disease.

Because the reCDV vaccine uses a novel vector, we tested the safety of this vaccine on reproductive polecat jills before conception, during pregnancy, and on kit growth 17–35 days postpartum as a prelude to vaccine use in reproductive black-footed ferrets. For 3 years, the National Black-footed Ferret Conservation Center has been vaccinating reproductive black-footed ferrets with PureVax starting several months prior to the breeding season. This practice has not caused any identifiable adverse effects on fecundity and overall production (P. Marinari, oral commun., 2004).

Vectored Vaccine Use in the Face of Passive Immunity

In 1997, 12 randomly selected Siberian polecat kits from mothers vaccinated twice with reCDV before conception and delivery (fig. 7, lower timeline) were themselves vaccinated at 4 and 6 weeks of age; kits received a standard challenge at 19 weeks of age.

All kits challenged at 19 weeks of age died with characteristic signs of CDV postchallenge. At this age, maternal protective immunity has disappeared in domestic ferrets (Gorham, 1999; Welter and others, 2000), suggesting that active immunization for CDV with reCDV (at $10^{5.5}$ PFU subcutaneously) in the presence of passive immunity, as tested in the present series, was without benefit.

Indirect evidence has suggested that antigen presentation to the cell-mediated arm of the immune system and particularly to T lymphocyte-induced cytotoxicity can lead to cell-mediated immunity independent of humoral responses (Siegrist and others, 1998a,b). It has been demonstrated in puppies (Taylor and others, 1994) that vectored vaccination with rabies glycoprotein results in active immunization in the face of blocking passive maternal antibodies. Here, we hypothesized that reCDV vaccine might actively protect young Siberian polecats postnatally even though they carried passive immune protection from circulating maternal antibodies generated against the same vaccine. According to this line of reasoning, active immunity would develop during postnatal vaccination with reCDV by independently augmenting active (mostly T cell-mediated) immunity. This possible application was attractive because maternal immunity typically blocks conventional vaccines during this period, and the actual trajectory of waning maternal immunity is unpredictable in mustelid kits (Gorham, 1999), leaving susceptible young unprotected. Welter and others (2000) challenged domestic ferrets at 12 weeks of age after parenteral vaccination with canarypox and vaccinia-vectored CDV vaccines for F and HA. In their study, vector-origin antigens had little effect on survival in early vaccinates, which was not significantly different from that of CDV-naïve controls. These results are similar to ours for the Siberian polecat, where early vaccinates, like CDV-naïve controls, succumbed to CDV during challenge. In their study, Welter and others (2000) attributed this vaccination failure to immaturity and nonresponsiveness of the immune system of the domestic ferret, a relatively altricial species. Our results support their observation; however, a lower dose of a canarypox-vectored vaccine was used in our study in Siberian polecats, complicating the final interpretation.

Canarypox cross-vaccination was not observed in unvaccinated Siberian polecats housed in adjacent cages. Thus, reCDV does not appear to be prone to cross-vaccination in this species. Similarly, reCDV vaccinated pregnant Siberian polecat jills adjacently caged with CDV and reCDV vector-naïve polecat jills never seroconverted following reCDV vaccination (J. Wimsatt, unpub. data., 1997).

Discussion

The ability of a vaccine to protect against differing CDV strains depends on how close the HA and F proteins are to the vaccine's Onderstepoort-origin proteins expressed by the vector. In this regard, Galaxy-D and the vectored (reCDV) vaccine are similar in the qualitative aspects of their protection. For the vectored vaccine, it is too early to assess the long-term effects of injecting canarypox into foreign species. In theory, the nature of recombinant vaccines and the limited antigens they express may require that they be updated more frequently to keep pace with strain changes, if other antigens can contribute to immune protection during modified-live infection and immunity development. If so, verified failure of antigenic protection with reCDV vaccines may potentially serve as a more exacting measure of evolving antigenic shifts in wild strains in the future.

In contrast to modified-live vaccination, vectored vaccine presentation to the mucosal membranes may yield different results from parenteral administration, reflecting limited vector invasiveness of mucosal surfaces, particularly in regards to the canarypox vector (Welter and others, 1999). Whether this will have a practical outcome, say in the heterogeneity of host responses across species following oral administration, remains to be determined. The long-term impact of live virus vectors and their potential to revert to virulence remains a matter of speculation, but careful monitoring is warranted, since poxviruses generally have the potential to mutate and adapt to new species. While replication of the canarypox virus in hosts appears to be minimal, the period of retention of the virus has not been as well characterized in varied species, and the large number of species receiving this vaccine leaves open the possibility of specific species predispositions and alterations in strain virulence over time, if persistence occurs. The recent emergence of a pathogenic variant of vaccinia virus may exemplify this concern (Palca, 2005).

What the Future May Hold

Considering the wide range of related morbilliviruses affecting diverse orders and classes of animals, and the demonstrated transfer of distemper and other morbilliviruses to bystander species (Stallknecht and others, 1991; Jacobson and others, 1992, 1997, 2001; Visser and others, 1993; Appel and Montali, 1994; Duignan and others, 1995; Richter and others, 1996; Karesh and others, 1997, 1999; Longbottom, 1997; Barrett, 1999; Jauniaux and others, 2000; Bossart and others, 2001; Lam and Chua, 2002; Johnson, 2003), the potential for cross-species movement and de novo creation of mutated variants of CDV seems high. For example, recent focus on HA variability among sympatric CDV strains (Gemma and others, 1996) suggests that commercial vaccine preparations may become inadequate for protection against CDV in the future (Mochizuki and others, 1999). However, caution is always warranted when documenting a vaccine failure because of the possibility of other causes. These other causes include incomplete dosing, genetic or ill-defined causes of host nonresponse (Leisewitz and others, 2001), administration during occult periods of host immunosuppression, and suboptimal product handling prior to use. Vaccine nonresponders have been documented for more than one canine disease (R. Schultz, oral commun., 2003).

A recent canine distemper outbreak at a zoo was associated with exposure to wild raccoons in the Chicago area (Lednicky and others, 2004). The appearance of this distinct strain has introduced some uncertainty about the ability of current commercial CDV vaccines to protect against new or emerging wildlife strains (Lednicky and others, 2004). Recent CDV disease outbreaks involving novel strains have raised the suspicion of vaccine failures although without controlled challenge studies these suspicions are difficult to prove (Bohm and others, 1989; Maes and others, 2003). Even so, this proposed causal relationship between novel strains, possibly from wildlife reservoirs, and the potential for vaccine failures has not been investigated adequately, employing careful ecological study techniques, modern molecular tools, and strain-specific challenge studies in vaccine-protected animals. An outbreak of naturally occurring CDV in black-footed ferrets highlights the need for safe and effective vaccines to protect them following reintroduction and as the threat continues into the future (Williams and others, 1988). Large cats and other carnivores would likely benefit as well (Blythe and others, 1983; Davidson and others, 1992; Appel and others, 1994; Harder and others, 1995; Roelke-Parker and others, 1996; Leisewitz and others, 2001).

The emergence of vaccine-resistant virus variants, like the analogous emergence of antibiotic-resistant bacteria, may be facilitated when vaccination is widely used and selection pressure is high. Even so, CDV vaccines have been surprisingly reliable over the last 50 years; this may relate to the observation that negative sense RNA viruses are less prone to recombine than other viruses (Chare and others, 2003).

Outbreaks of canine distemper in distant parts of the world have highlighted the significance of domestic and wildlife reservoirs as purveyors of distemper-induced disease worldwide (Bohm and others, 1989). Recent investigations surrounding CDV outbreaks in Japan (Mochizuki and others, 1999), Denmark (Blixenkrone-Moller and others, 1993), Poland (Jozwik and Frymus, 2002), and the United States (Lednicky and others, 2004) have brought into the focus the possible emergence of CDV strains no longer optimally immunized with commercial vaccine products. For the most part, such strains have shown characteristic heterogeneity in the HA gene, while the F component of current wild strains has remained surprisingly uniform across strains. This situation is analogous to using measles vaccination to cross-protect against CDV (Chalmers and Baxendale, 1994). When CDV passes across species, the possibility of variability at all sites, including the F protein gene, seems highly likely as new hosts tend to cause selection for greater virus diversity (Woolhouse and others, 2001). In related paramyxoviruses affecting other species, F gene heterogeneity has been noted and may influence species predilections, disease phenotypy, and vaccine efficacy in the future, especially under strong selection pressure (Collins and others, 1998; Ning and others, 2002; Ujvári and others, 2003).

The Promise of New Vaccine Strategies

A recent efficacy study using an adenovirus-vectored vaccine demonstrated the development of significant active immunity against CDV with the absence of mucosal immunity against the adenovirus vector in domestic puppies (Fischer and others, 2002). None of the other available vectored CDV vaccines are satisfactory for immunization of very young carnivores, and the adenovirus vector appears superior in this regard.

DNA vaccines are relatively safe, simple, and cheap to produce. They consist of DNA-encoding genes capable of producing vaccine antigens in host cells and mammalian promoters leading to selected gene expression (Liu, 2003). Recently, new DNA vaccines administered intramuscularly were shown to be highly effective against severe CDV challenge in mice (Sixt and others, 1998) and dogs (Fischer and others, 2003).

Unfortunately, nonparenteral methods of DNA vaccine and vectored vaccine delivery have low efficiency in producing a protective immune response. The low oral efficiency of the canarypox vector (Wimsatt and others, 2003) limits the potential use of commercial products now available

(Merial Technical Services, oral commun., 2004). Even so, a significant serological response was observed following oral administration (T. Vickers, oral commun., 2005) of two Pure-Vax vaccine doses at once in a recent study of Channel Island gray foxes (*Urocyon littoralis*) (Vickers and others, 2004). Vaccinia-vectored CDV constructs exist for research use (J. Taylor, oral commun., 1998). Vaccinia constructs appear to have greater enteric efficiency for bait delivery, as has been demonstrated during the use of Raboral V-RG in public health programs to vaccinate wild carnivores against rabies and experimentally with a vaccinia-vectored CDV vaccine (Welter and others, 1999). Mucosal delivery of DNA vaccines via new designer carriers will likely provide new opportunities for oral DNA vaccine delivery in the future (Hobson and others, 2003). With the advent of antiviral drugs, viral inhibitors of virus-host cell F are being developed to moderate paramyxovirus-induced disease progression, providing a new therapeutic approach (De Clercq, 2002).

The relatively homozygous (genetically depauperate) black-footed ferret is at risk of CDV-induced disease with the use of any currently available modified-live products. With the advent of designer vaccines for the concurrent delivery of immunostimulatory genes in concert with immunogens, the ability to stimulate the immune system (e.g., to express immunostimulatory levels of interleukin-6) while vaccinating will offer new possibilities in the future. Even the ability to correct an identified interleukin-6 deficiency in the black-footed ferret may be on the horizon through the use of gene therapy via vectored vaccine or naked DNA approaches. Such methods could eventually serve to enhance the resistance of this and other sensitive species to the ravages of infectious diseases, if germ line incorporation becomes practical.

References Cited

Adams, G.L., Ford, R.B., Gershwin, L.J., and Schultz, R.D., 1997, Recombinant vaccine technology: Compendium on Continuing Education for the Practicing Veterinarian, supplement, v. 19, p. 1–16.

Anonymous, 1978, Multiple sclerosis, canine distemper, and measles immunisation: Lancet, v. 1, p. 1204–1205.

Appel, M., and Robson, D.S., 1973, A microneutralization test for canine distemper virus: American Journal of Veterinary Research, v. 34, p. 1459–1463.

Appel, M.J., Glickman, L.T., Raine, C.S., and Tourtellotte, W.W., 1981, Canine viruses and multiple sclerosis: Neurology, v. 31, p. 944–949.

Appel, M.J., Reggiardo, C., Summers, B.A., Pearce-Kelling, S., Mare, C.J., Noon, T.H., Reed, R.E., Shively, J.N., and Orvell, C., 1991, Canine distemper virus infection and encephalitis in javelinas (collared peccaries): Archives of Virology, v. 119, p. 147–152.

Appel, M.J., and Summers, B.A., 1995, Pathogenicity of morbilliviruses for terrestrial carnivores: Veterinary Microbiology, v. 44, p. 187–191.

Appel, M.J., Yates, R.A., Foley, G.L., Bernstein, J.J., Santinelli, S., Spelman, L.H., Miller, L.D., Arp, L.H., Anderson, M., and Barr, M., 1994, Canine distemper epizootic in lions, tigers, and leopards in North America: Journal of Veterinary Diagnosis and Investigation, v. 6, p. 277–288.

Appel, M.J.G., and Montali, R.J., 1994, Canine distemper and emerging morbillivirus diseases in exotic species: American Association of Zoo Veterinarians, Annual Proceedings, p. 336–339.

Arjo, W.M., Gese, E.M., Bromley, C., Kozlowski, A., and Williams, E.S., 2003, Serologic survey for diseases in free-ranging coyotes (*Canis latrans*) from two ecologically distinct areas of Utah: Journal of Wildlife Diseases, v. 39, p. 449–455.

Axthelm, M.K., and Krakowka, S., 1998, Experimental old dog encephalitis (ODE) in a gnotobiotic dog: Veterinary Pathology, v. 35, p. 527–534.

Barrett, T., 1999, Morbillivirus infections, with special emphasis on morbilliviruses of carnivores: Veterinary Microbiology, v. 69, p. 3–13.

Barrett, T., Visser, I., Mamaev, L., Goatley, L., Van Bressem, M-F., and Osterhaus, A., 1993, Dolphin and porpoise morbilliviruses are genetically distinct from phocine distemper virus: Virology, v. 193, p. 1010–1021.

Bencsik, A., Malcus, C., Akaoka, H., Giraudon, P., Belin, M.F., and Bernard, A., 1996, Selective induction of cytokines in mouse brain infected with canine distemper virus—structural, cellular and temporal expression: Journal of Neuroimmunology, v. 65, p. 1–9.

Blixenkrone-Moller, M., Svansson, V., Have, P., Orvell, C., Appel, M., Pedersen, I.R., Dietz, H.H., and Henriksen, P., 1993, Studies on manifestations of canine distemper virus infection in an urban dog population: Veterinary Microbiology, v. 37, p. 163–173.

Blythe, L.L., Schmitz, J.A., Roelke, M., and Skinner, S., 1983, Chronic encephalomyelitis caused by canine distemper virus in a Bengal tiger: Journal of the American Veterinary Medical Association, v. 183, p. 1159–1162.

Bohm, J., Blixenkrone-Moller, M., and Lund, E., 1989, A serious outbreak of canine distemper among sled-dogs in northern Greenland: Arctic Medical Research, v. 48, p. 195–203.

Bossart, K.N., Wang, L.F., Eaton, B.T., and Broder, C.C., 2001, Functional expression and membrane fusion tropism of the envelope glycoproteins of Hendra virus: Virology, v. 290, p. 121–135.

Bronson, E., Denver, M., Karim, B., Fitzgerald, S., Wise, A.G., and Maes, R., 2003, Vaccine-induced canine distemper virus infection in a lesser panda (*Ailurus fulgens fulgens*) three years following last vaccination: American Association of Zoo Veterinarians, Annual Proceedings, p. 185–186.

Burger, D., and Gorham, J.R., 1964, Response of ferrets and mink to vaccination with chicken embryo-adapted distemper virus: Archiv Gesamte Virusforsch, v. 15, p. 449–461.

Bush, M., Montali, R.J., Brownstein, D., James, A.E., Jr., and Appel, M.J., 1976, Vaccine-induced canine distemper in a lesser panda: Journal of the American Veterinary Medical Association, v. 169, p. 959–960.

Cabasso, V.J., and Cox, H.R., 1953, Onset of resistance and duration of immunity to distemper in ferrets following a single injection of avianized distemper vaccine: Veterinary Medicine, v. 48, p. 147–150.

Carpenter, J.W., Appel, M.J., Erickson, R.C., and Novilla, M.N., 1976, Fatal vaccine-induced canine distemper virus infection in black-footed ferrets: Journal of the American Veterinary Medical Association, v. 169, p. 961–964.

Carpenter, M.A., Appel, M.J., Roelke-Parker, M.E., Munson, L., Hofer, H., East, M., and O'Brien, S.J., 1998, Genetic characterization of canine distemper virus in Serengeti carnivores: Veterinary Immunology and Immunopathology, v. 65, p. 259–266.

Cartwright, E.J., Gordon, M.T., Freemont, A.J., Anderson, D.C., and Sharpe, P.T., 1993, Paramyxoviruses and Paget's disease: Journal of Medical Virology, v. 40, p. 133–141.

Chalmers, W.S., and Baxendale, W., 1994, A comparison of canine distemper vaccine and measles vaccine for the prevention of canine distemper in young puppies: Veterinary Record, v. 135, p. 349–353.

Chare, E.R., Gould, E.A., and Holmes, E.C., 2003, Phylogenetic analysis reveals a low rate of homologous recombination in negative-sense RNA viruses: Journal of General Virology, v. 84, p. 2691–2703.

Collins, M.S., Franklin, S., Strong, I., Meulemans, G., and Alexander, D.J., 1998, Antigenic and phylogenetic studies on a variant Newcastle disease virus using anti-fusion protein monoclonal antibodies and partial sequencing of the F protein gene: Avian Pathology, v. 27, p. 90–96.

Cook, S.D., Blumberg, B., and Dowling, P.C., 1986, Potential role of paramyxoviruses in multiple sclerosis: Neurologic Clinics, v. 4, p. 303–319.

Cypher, B.L., Scrivner, J.H., Hammer, K.L., and O'Farrell, T.P., 1998, Viral antibodies in coyotes from California: Journal of Wildlife Diseases, v. 34, p. 259–264.

Davidson, W.R., Nettles, V.F., Hayes, L.E., Howerth, E.W., and Couvillion, C.E., 1992, Diseases diagnosed in gray foxes (*Urocyon cinereoargenteus*) from the southeastern United States: Journal of Wildlife Diseases, v. 28, p. 28–33.

De Clercq, E., 2002, Highlights in the development of new antiviral agents: Mini Reviews in Medicinal Chemistry, v. 2, p. 163–175.

De Keyser, J., Wilczak, N., Walter, J.H., and Zurbriggen, A., 2001, Disappearance of beta2-adrenergic receptors on astrocytes in canine distemper encephalitis—possible implications for the pathogenesis of multiple sclerosis: Neuroreport, v. 12, p. 191–194.

Dhurandhar, N.V., 2001, Infectobesity—obesity of infectious origin: Journal of Nutrition, v. 131, p. 2794S–2797S.

Duignan, P.J., House, C., Geraci, J.R., Duffy, N., Rima, B.K., Walsh, M.T., Early, G., St. Aubin, D.J., Sadove, S., Koopman, H., and Rhinehart, H., 1995, Morbillivirus infection in cetaceans of the western Atlantic: Veterinary Microbiology, v. 44, p. 241–249.

Dunbar, M.R., Cunningham, M.W., and Roof, J.C., 1998, Seroprevalence of selected disease agents from free-ranging black bears in Florida: Journal of Wildlife Diseases, v. 34, p. 612–619.

Dyken, P.R., 2001, Neuroprogressive disease of post-infectious origin—a review of a resurging subacute sclerosing panencephalitis (SSPE): Mental Retardation and Developmental Disabilities Research Reviews, v. 7, p. 217–225.

Etchart, N., Desmoulins, P-O., Chemin, K., Maliszewski, C., Dubois, B., Wild, F., and Kaiserlian, D., 2001, Dendritic cells recruitment and in vivo priming of CD8$^+$ CTL induced by a single topical or transepithelial immunization via the buccal mucosa with measles virus nucleoprotein: Journal of Immunology, v. 167, p. 384–391.

Evans, M.B., Bunn, T.O., Hill, H.T., and Platt, K.B., 1991, Comparison of in vitro replication and cytopathology caused by strains of canine distemper virus of vaccine and field origin: Journal of Veterinary Diagnostic Investigation, v. 3, p. 127–132.

Farrell, R.K., Skinner, S.F., Gorham, J.R., and Lauerman, L.H., 1971, The aerosol and subcutaneous administration of attenuated egg adapted distemper vaccine to ferret kits from distemper immune females: Research in Veterinary Sciences, v. 12, p. 392–393.

Fearneyhough, M.G., Wilson, P.J., Clark, K.A., Smith, D.R., Johnston, D.H., Hicks, B.N., and Moore, G.M., 1998, Results of an oral rabies vaccination program for coyotes:

Journal of the American Veterinary Medical Association, v. 212, p. 498–502.

Fischer, L., Tronel, J.P., Minke, J., Barzu, S., Baudu, P., and Audonnet, J.C., 2003, Vaccination of puppies with a lipid-formulated plasmid vaccine protects against a severe canine distemper virus challenge: Vaccine, v. 21, p. 1099–1102.

Fischer, L., Tronel, J.P., Pardo-David, C., Tanner, P., Colombet, G., Minke, J., and Audonnet, J.C., 2002, Vaccination of puppies born to immune dams with a canine adenovirus-based vaccine protects against a canine distemper virus challenge: Vaccine, v. 20, p. 3485–3497.

Fox, J., Pearson, R., and Gorham, J., 1998, Viral diseases, *in* Fox, J.G., ed., Biology and diseases of the ferret (2d ed.): Baltimore, Md., Williams and Wilkins, Chap. 15, p. 355–360.

Fraser, W.D., 1997, Paget's disease of bone: Current Opinions in Rheumatology, v. 9, p. 347–354.

Friedrichs, W.E., Reddy, S.V., Bruder, J.M., Cundy, T., Cornish, J., Singer, F.R., and Roodman, G.D., 2002, Sequence analysis of measles virus nucleocapsid transcripts in patients with Paget's disease: Journal of Bone and Mineral Research, v. 17, p. 145–151.

Garg, R.K., 2002, Subacute sclerosing panencephalitis: Postgraduate Medical Journal, v. 78, p. 63–70.

Gemma, T., Watari, T., Akiyama, K., Miyashita, N., Shin, Y.S., Iwatsuki, K., Kai, C., and Mikami, T., 1996, Epidemiological observations on recent outbreaks of canine distemper in Tokyo area: Journal of Veterinary Medical Sciences, v. 58, p. 547–550.

Gese, E.M., Schultz, R.D., Johnson, M.R., Williams, E.S., Crabtree, R.L., and Ruff, R.L., 1997, Serological survey for diseases in free-ranging coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: Journal of Wildlife Diseases, v. 33, p. 47–56.

Gese, E.M., Schultz, R.D., Rongstad, O.J., and Andersen, D.E., 1991, Prevalence of antibodies against canine parvovirus and canine distemper virus in wild coyotes in southeastern Colorado: Journal of Wildlife Diseases, v. 27, p. 320–323.

Gorham, J.R., 1966, Duration of vaccination immunity and the influence on subsequent prophylaxis: Journal of the American Veterinary Medical Association, v. 149, p. 699–704.

Gorham, J.R., 1999, Some experiments and field observations of distemper in mink and ferrets: Advances in Veterinary Medicine, v. 41, p. 557–570.

Greenacre, C.B., 2003, Incidence of adverse events in ferrets vaccinated with distemper or rabies vaccine: 143 cases (1995–2001): Journal of the American Veterinary Medical Association, v. 223, p. 663–665.

Greene, C.E., and Appel, M.J.G., 1998, Canine distemper, *in* Greene, C.E., Infectious diseases of the dog and cat: Philadelphia, Pa., W.B. Saunders, Chap. 3, p. 9–22.

Grinder, M., and Krausman, P.R., 2001, Morbidity-mortality factors and survival of an urban coyote population in Arizona: Journal of Wildlife Diseases, v. 37, p. 312–317.

Grone, A., Fonfara, S., and Baumgartner, W., 2002, Cell type-dependent cytokine expression after canine distemper virus infection: Viral Immunology, v. 15, p. 493–505.

Guo, W., Evermann, J.F., Foreyt, W.J., Knowlton, F.F., and Windberg, L.A., 1986, Canine distemper virus in coyotes—a serologic survey: Journal of the American Veterinary Medical Association, v. 189, p. 1099–1100.

Hagen, K.W., Goto, H., and Gorham, J.R., 1970, Distemper vaccine in pregnant ferrets and mink: Research in Veterinary Sciences, v. 11, p. 458–460.

Halbrooks, R.D., Swango, L.J., Schnurrenberger, P.R., Mitchell, F.E., and Hill, E.P., 1981, Response of grey foxes to modified-live virus canine distemper vaccines: Journal of the American Veterinary Medical Association, v. 179, p. 1170–1174.

Hall, W.W., Imagawa, D.T., and Choppin, P.W., 1979, Immunological evidence for the synthesis of all canine distemper virus polypeptides in chronic neurological diseases in dogs—chronic distemper and old dog encephalitis differ from SSPE in man: Virology, v. 98, p. 283–287.

Hanlon, C.A., Niezgoda, M., Hamir, A.N., Schumacher, C., Koprowski, H., and Rupprecht, C.E., 1998, First North American field release of vaccinia-rabies glycoprotein recombinant virus: Journal of Wildlife Diseases, v. 34, p. 228–239.

Harder, T.C., Kenter, M., Appel, M.J., Roelke-Parker, M.E., Barrett, T., and Osterhaus, A.D., 1995, Phylogenetic evidence of canine distemper virus in Serengeti's lions: Vaccine, v. 13, p. 521–523.

Harrus, S., Waner, T., Aizenberg, I., Safra, N., Mosenco, A., Radoshitsky, M., and Bark, H., 2002, Development of hypertrophic osteodystrophy and antibody response in a litter of vaccinated Weimaraner puppies: Journal of Small Animal Practice, v. 43, p. 27–31.

Hashimoto, M., Une, Y., and Mochizuki, M., 2001, Hemagglutinin genotype profiles of canine distemper virus from domestic dogs in Japan: Archives of Virology, v. 146, p. 149–155.

Hernan, M.A., Zhang, S.M., Lipworth, L., Olek, M.J., and Ascherio, A., 2001, Multiple sclerosis and age at infection with common viruses: Epidemiology, v. 12, p. 301–306.

Hobson, P., Barnfield, C., Barnes, A., and Klavinskis, L.S., 2003, Mucosal immunization with DNA vaccines: Methods, v. 31, p. 217–224.

Hoyland, J.A., Dixon, J.A., Berry, J.L., Davies, M., Selby, P.L., and Mee, A.P., 2003, A comparison of in situ hybridisation, reverse transcriptase-polymerase chain reaction (RT-PCR) and in situ-RT-PCR for the detection of canine distemper virus RNA in Paget's disease: Journal of Virological Methods, v. 109, p. 253–259.

Ikeda, Y., Nakamura, K., Miyazawa, T., Chen, M.C., Kuo, T.F., Lin, J.A., Mikami, T., Kai, C., and Takahashi, E., 2001, Seroprevalence of canine distemper virus in cats: Clinical Diagnostics and Laboratory Immunology, v. 8, p. 641–644.

Itakura, C., Nakamura, K., Nakatsuka, J., and Goto, M., 1979, Distemper infection in lesser pandas due to administration of a canine distemper live vaccine: Nippon Juigaku Zasshi, v. 41, p. 561–566.

Jacobson, E.R., Adams, H.P., Geisbert, T.W., Tucker, S.J., Hall, B.J., and Homer, B.L., 1997, Pulmonary lesions in experimental ophidian paramyxovirus pneumonia of Aruba Island rattlesnakes, *Crotalus unicolor*: Veterinary Pathology, v. 34, p. 450–459.

Jacobson, E.R, Gaskin, J.M., Wells, S., Bowler, K., and Schumacher, J., 1992, Epizootic of ophidian paramyxovirus in a zoological collection—pathological, microbiological, and serological findings: Journal of Zoo and Wildlife Medicine, v. 23, p. 318–327.

Jacobson, E.R., Origgi, F., Pessier, A.P., Lamirande, E.W., Walker, I., Whitaker, B., Stalis, I.H., Nordhausen, R., Owens, J.W., and Nichols, D.K., 2001, Paramyxovirus infection in caiman lizards (*Draecaena guianensis*): Journal of Veterinary Diagnostic Investigation, v. 13, p. 143–151.

Jauniaux, T., Charlier, G., Desmecht, M., Haelters, J., Jacques, T., Losson, B., Van Gompel, J., Tavernier, J., and Coignoul, F., 2000, Pathological findings in two fin whales (*Balaenoptera physalus*) with evidence of morbillivirus infection: Journal of Comparative Pathology, v. 123, p. 198–201.

Johnson, R.T., 2003, Emerging viral infections of the nervous system: Journal of NeuroVirology, v. 9, p. 140–147.

Jozwik, A., and Frymus, T., 2002, Natural distemper in vaccinated and unvaccinated dogs in Warsaw: Journal of Veterinary Medicine, Series B, Infectious Diseases and Veterinary Public Health, v. 49, p. 413–414.

Karesh, W.B., del Campo, A., Braselton, W.E., Puche, H., and Cook, R.A., 1997, Health evaluation of free-ranging and hand-reared macaws (*Ara* spp.) in Peru: Journal of Zoo and Wildlife Medicine, v. 28, p. 368–377.

Karesh, W.B., Uhart, M.M., Frere, E., Gandini, P., Braselton, W.E., Puche, H., and Cook, R.A., 1999, Health evaluation of free-ranging rockhopper penguins (*Eudyptes chrysocomes*) in Argentina: Journal of Zoo and Wildlife Medicine, v. 30, p. 25–31.

Kennedy, S., Kuiken, T., Jepson, P.D., Deaville, R., Forsyth, M., Barrett, T., van de Bildt, M.W., Osterhaus, A.D., Eybatov, T., and Duck, C., 2000, Mass die-off of Caspian seals caused by canine distemper virus: Emerging Infectious Diseases, v. 6, p. 637–639.

Krakowka, S., 1982, Mechanisms of in vitro immunosuppression in canine distemper virus infection: Journal of Clinical Laboratory Immunology, v. 8, p. 187–196.

Krakowka, S., Confer, A., and Koestner, A., 1974, Evidence for transplacental transmission of canine distemper virus—two case reports: American Journal of Veterinary Research, v. 35, p. 1251–1253.

Krakowka, S., Hoover, E.A., Koestner, A., and Ketring, K., 1977, Experimental and naturally occurring transplacental transmission of canine distemper virus: American Journal of Veterinary Research, v. 38, p. 919–922.

Krakowka, S., Ringler, S.S., Lewis, M., Olsen, R.G., and Axthelm, M.K., 1987, Immunosuppression by canine distemper virus—modulation of in vitro immunoglobulin synthesis, interleukin release and prostaglandin E2 production: Veterinary Immunology and Immunopathology, v. 15, p. 181–201.

Lam, S.K., and Chua, K.B., 2002, Nipah virus encephalitis outbreak in Malaysia: Clinical Infectious Diseases, v. 34, Suppl. 2, p. S48–S51.

Lednicky, J., Dubach, J., Kinsel, M.J., Meehan, T.P., Bocchetta, M., Hungerford, L.L., Sarich, N.A., Witecki, K.E., Braid, M.D., Pedrak, C., and Houde, C.M., 2004, Genetically distant canine distemper virus lineages have recently caused epizootics with somewhat different characteristics in raccoons living around a large suburban zoo in the USA: Virology Journal, v. 1, http://www.virologyj.com/content/1/1/2.

Leisewitz, A.L., Carter, A., Van Vuuren, M., and Van Blerk, L., 2001, Canine distemper infections, with special reference to South Africa, with a review of the literature: Journal of South African Veterinary Association, v. 72, p. 127–136.

Liashenko, V.A., Krasnova, V.P., and Youminova, N.V., 1999, Measles IgA in the nasal washings of adult volunteers and children immunized intranasally with measles vaccine L-16: Human Antibodies, v. 9, p. 143–148.

Lincoln, S.D., Gorham, J.R., Ott, R.L., and Hegreberg, G.A., 1971, Etiologic studies of old dog encephalitis. I. Demonstration of canine distemper viral antigen in the brain in two cases: Veterinary Pathology, v. 8, p. 1–8.

Liu, M.A., 2003, DNA vaccines—a review: Journal of Internal Medicine, v. 253, p. 402–410.

Longbottom, H., 1997, Emerging infectious diseases: Communicable Diseases Intelligence, v. 21, p. 89–93.

Macy, D.W., and Couto, C.G., 2001, Prevention and treatment of injection-site sarcomas: Journal of Feline Medicine and Surgery, v. 3, p. 169–170.

Maes, R.K., Wise, A.G., Fitzgerald, S.D., Ramudo, A., Kline, J., Vilnis, A., and Benson, C., 2003, A canine distemper outbreak in Alaska—diagnosis and strain characterization using sequence analysis: Journal of Veterinary Diagnostic Investigation, v. 15, p. 213–220.

Mee, A.P., Dixon, J.A., Hoyland, J.A., Davies, M., Selby, P.L., and Mawer, E.B., 1998, Detection of canine distemper virus in 100% of Paget’s disease samples by in situ-reverse transcriptase-polymerase chain reaction: Bone, v. 23, p. 171–175.

Mee, A.P., Gordon, M.T., May, C., Bennett, D., Anderson, D.C., and Sharpe, P.T., 1993, Canine distemper virus transcripts detected in the bone cells of dogs with metaphyseal osteopathy: Bone, v. 14, p. 59–67.

Meertens, N., Stoffel, M.H., Cherpillod, P., Wittek, R., Vandevelde, M., and Zurbriggen, A., 2003, Mechanism of reduction of virus release and cell-cell fusion in persistent canine distemper virus infection: Acta Neuropathologica, v. 106, p. 303–310.

Mochizuki, M., Hashimoto, M., Hagiwara, S., Yoshida, Y., and Ishiguro, S., 1999, Genotypes of canine distemper virus determined by analysis of the hemagglutinin genes of recent isolates from dogs in Japan: Journal of Clinical Microbiology, v. 37, p. 2936–2942.

Montali, R.J., Bartz, C.R., Teare, J.A., Allen, J.T., Appel, M.J., and Bush, M., 1983, Clinical trials with canine distemper vaccines in exotic carnivores: Journal of the American Veterinary Medical Association, v. 183, p. 1163–1167.

Montali, R.J., Tell, L., Bush, M., Cambre, R.C., Kenny, D., Sutherland-Smith, M., and Appel, M.J.G., 1994, Vaccination against canine distemper in exotic carnivores—successes and failures: American Association of Zoo Veterinarians, Annual Proceedings, p. 340–344.

Moro, L., de Sousa Martins, A., de Moraes Alves, C., de Araujo Santos, F.G., dos Santos Nunes, J.E., Carneiro, R.A., Carvalho, R., and Vasconcelos, A.C., 2003a, Apoptosis in canine distemper: Archives of Virology, v. 148, p. 153–164.

Moro, L., Martins, A.S., Alves, C.M., Santos, F.G., Del Puerto, H.L., and Vasconcelos, A.C., 2003b, Apoptosis in the cerebellum of dogs with distemper: Journal of Veterinary Medicine, Part B, Infectious Diseases of Veterinary Public Health, v. 50 p. 221–225.

Newman, S.J., Johnson, R., Sears, W., and Wilcock, B., 2002, Investigation of repeated vaccination as a possible cause of glomerular disease in mink: Canadian Journal of Veterinary Research, v. 66, p. 158–164.

Ning, X., Ayata, M., Kimura, M., Komase, K., Furukawa, K., Seto, T., Ito, N., Shingai, M., Matsunaga, I., and Yamano, T., 2002, Alterations and diversity in the cytoplasmic tail of the fusion protein of subacute sclerosing panencephalitis virus strains isolated in Osaka, Japan: Virus Research, v. 86, p. 123–131.

Noon, T.H., Heffelfinger, J.R., Olding, R.J., Wesche, S.L., and Reggiardo, C., 2003, Serologic survey for antibodies to canine distemper virus in collared peccary (*Tayassu tajacu*) populations in Arizona: Journal of Wildlife Diseases, v. 39, p. 221–223.

O’Brien, S.J., Martenson, J.S., Eichelberger, M.A., Thorne, E.T., and Wright, F., 1989, Genetic variation and molecular systematics of the black-footed ferret, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 21–33.

Ogra, P.L., Fishaut, M., and Gallagher, M.R., 1980, Viral vaccination via the mucosal routes: Reviews of Infectious Diseases, v. 2, p. 352–369.

Olson, C.A., and Werner, P.A., 1999, Oral rabies vaccine contact by raccoons and nontarget species in a field trial in Florida: Journal of Wildlife Diseases, v. 35, p. 687–695.

Palca, J., 2005, Flu-like disease in Brazil puzzles experts: NPR, Nov. 10, 2005.

Paoletti, E., Tartaglia, J., and Cox, W.I., 1993, Immunotherapeutic strategies for cancer using poxvirus vectors: Annals of the New York Academy of Sciences, v. 690, p. 292–300.

Paoletti, E., Tartaglia, J., and Taylor, J., 1994, Safe and effective poxvirus vectors—NYVAC and ALVAC: Development of Biological Standards, v. 82, p. 65–69.

Paoletti, E., Taylor, J., Meignier, B., Meric, C., and Tartaglia, J., 1995, Highly attenuated poxvirus vectors—NYVAC, ALVAC and TROVAC: Development of Biological Standards, v. 84, p. 159–163.

Perkus, M.E., Tartaglia, J., and Paoletti, E., 1995a, Poxvirus-based vaccine candidates for cancer, AIDS, and other infectious diseases: Journal of Leukocyte Biology, v. 58, p. 1–13.

Perkus, M.E., Taylor, J., Tartaglia, J., Pincus, S., Kauffman, E.B., Tine, J.A., and Paoletti, E., 1995b, Live attenuated vaccinia and other poxviruses as delivery systems—public health issues: Annals of the New York Academy of Sciences, v. 754, p. 222–233.

Pincus, S., Tartaglia, J., and Paoletti, E., 1995, Poxvirus-based vectors as vaccine candidates: Biologicals, v. 23, p. 159–164.

Pollack, J.D., 2001, Caspian seal die-off is caused by canine distemper virus: Trends in Microbiology, v. 9, p. 108.

Povey, R.C., 1986, Persistent viral infection. The carrier state: Veterinary Clinics of North America, Small Animal Practice, v. 16, p. 1075–1095.

Richter, G.A., Homer, B.L., Moyer, S.A., Williams, D.S., Scherba, G., Tucker, S.J., Hall, B.J., Pedersen, J.C., and Jacobson, E.R., 1996, Characterization of paramyxoviruses isolated from three snakes: Virus Research, v. 43, p. 77–83.

Rima, B.K., Baczko, K., Imagawa, D.T., and ter Meulen, V., 1987, Humoral immune response in dogs with old dog encephalitis and chronic distemper meningo-encephalitis: Journal of General Virology, v. 68, p. 1723–1735.

Rockborn, G., 1957, Viraemia and neutralizing antibodies in naturally acquired distemper in dogs: Archiv Gesamte Virusforsch, v. 7, p. 183–190.

Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O'Brien, S.J., Pospischil, A., Hofmann-Lehmann, R., and Lutz, H., 1996, A canine distemper virus epidemic in Serengeti lions (*Panthera leo*): Nature, v. 379, p. 441–445.

Rupprecht, C.E., Blass, L., Smith, K., Orciari, L.A., Niezgoda, M., Whitfield, S.G., Gibbons, R.V., Guerra, M., and Hanlon, C.A., 2001, Human infection due to recombinant vaccinia-rabies glycoprotein virus: New England Journal of Medicine, v. 345, p. 582–586.

Rzezutka, A., and Mizak, B., 2002, Application of N-PCR for diagnosis of distemper in dogs and fur animals: Veterinary Microbiology, v. 88, p. 95–103.

Saliki, J.T., Cooper, E.J., and Gustavson, J.P., 2002, Emerging morbillivirus infections of marine mammals—development of two diagnostic approaches: Annals of the New York Academy of Sciences, v. 969, p. 51–59.

Schlender, J., Schnorr, J-J., Spielhofer, P., Cathomen, T., Cattaneo, R., Billeter, M., ter Meulen, V., and Schneider-Schaulies, S., 1996, Interaction of measles virus glycoproteins with the surface of uninfected peripheral blood lymphocytes induces immunosuppression *in vitro*: Proceedings of the National Academy of Sciences, v. 93, p. 13194–13199.

Schneider-Schaulies, J., ter Meulen, V., and Schneider-Schaulies, S., 2003, Measles infection of the central nervous system: Journal of NeuroVirology, v. 9, p. 247–252.

Schultz, R.D., 1976, Failure of attenuated canine distemper virus (Rockborn strain) to suppress lymphocyte blastogenesis in dogs: Cornell Veterinarian, v. 66, p. 27–31.

Schultz, R., and Zuba, J., 2003, Understanding the basic principles and practical aspects of vaccinology: American Association of Zoo Veterinarians, Annual Proceedings, p. 162–178.

Siegrist, C.A., Barrios, C., Martinez, X., Brandt, C., Berney, M., Cordova, M., Kovarik, J., and Lambert, P.H., 1998a, Influence of maternal antibodies on vaccine responses—inhibition of antibody but not T cell responses allows successful early prime-boost strategies in mice: European Journal of Immunology, v. 28, p. 4138–4148.

Siegrist, C.A., Saddallah, F., Tougne, C., Martinez, X., Kovarik, J., and Lambert, P.H., 1998b, Induction of neonatal TH1 and CTL responses by live viral vaccines—a role for replication patterns within antigen presenting cells?: Vaccine, v. 16, p. 1473–1478.

Sixt, N., Cardoso, A., Vallier, A., Fayolle, J., Buckland, R., and Wild, T.F., 1998, Canine distemper virus DNA vaccination induces humoral and cellular immunity and protects against a lethal intracerebral challenge: Journal of Virology, v. 72, p. 8472–8476.

Stallknecht, D.E., Senne, D.A., Zwank, P.J., Shane, S.M., and Kearney, M.T., 1991, Avian paramyxoviruses from migrating and resident ducks in coastal Louisiana: Journal of Wildlife Diseases, v. 27, p. 123–128.

Stern, L.B., Greenberg, M., Gershoni, J.M., and Rozenblatt, S., 1995, The hemagglutinin envelope protein of canine distemper virus (CDV) confers cell tropism as illustrated by CDV and measles virus complementation analysis: Journal of Virology, v. 69, p. 1661–1668.

Stoskopf-Kennedy, S., Horsman, A.E., and Burns, R.B., 1997, Absence of interleukin-6 (IL-6) expression in the black-footed ferret (*Mustela nigripes*) [abs.]: 7th Congress of the International Society of Developmental and Comparative Immunology: Williamsburg, Va., College of William and Mary, p. 217.

Sutherland-Smith, M.R., Rideout, B.A., Mikolon, A.B., Appel, M.J., Morris, P.J., Shima, A.L., and Janssen, D.J., 1997, Vaccine-induced canine distemper in European mink, *Mustela lutreola*: Journal of Zoo and Wildlife Medicine, v. 28, p. 312–318.

Svansson, V., Blixenkrone-Moller, M., Skirnisson, K., Have, P., Heje, N.I., Nielsen, J., and Lund, E., 1993, Infection studies with canine distemper virus in harbour seals: Archives of Virology, v. 131, p. 349–359.

Tartaglia, J., Cox, W.I., Taylor, J., Perkus, M., Riviere, M., Meignier, B., and Paoletti, E., 1992, Highly attenuated poxvirus vectors: AIDS Research and Human Retroviruses, v. 8, 1445–1447.

Tartaglia, J., Pincus, S., and Paoletti, E., 1990, Poxvirus-based vectors as vaccine candidates: Critical Reviews in Immunology, v. 10, p. 13–30.

Tartaglia, J., Taylor, J., Cox, W.I., Audonnet, J., Perkus, M.E., Paoletti, E., Radaelli, A., Morghen, C., Meignier, B., and Riviere, M., 1993, Novel poxvirus strains as research tools and vaccine vectors, *in* Koff, W.C., Wong-Staal, F., and Kennedy, R.C., eds., AIDS Research Reviews: New York, Marcel-Dekker, Inc., p. 361–378.

Taylor, J., Tartaglia, J., Riviere, M., Duret, C., Languet, B., Chappuis, G., and Paoletti, E., 1994, Applications of canarypox (ALVAC) vectors in human and veterinary vaccination: Development of Biological Standards, v. 82, p. 131–135.

Tipold, A., Moore, P., Zurbriggen, A., Burgener, I., Barben, G., and Vandevelde, M., 1999, Early T cell response in the central nervous system in canine distemper virus infection: Acta Neuropathologica, v. 97, p. 45–56.

Tobler, L.H., and Imagawa, D.T., 1984, Mechanism of persistence with canine distemper virus—difference between a laboratory strain and an isolate from a dog with chronic neurological disease: Intervirology, v. 21, p. 77–86.

Truyen, U., Muller, T., Heidrich, R., Tackmann, K., and Carmichael, L.E., 1998, Survey on viral pathogens in wild red foxes (*Vulpes vulpes*) in Germany with emphasis on parvoviruses and analysis of a DNA sequence from a red fox parvovirus: Epidemiology and Infection, v. 121, p. 433–440.

Ujvári, D., Wehmann, E., Kaleta, E.F., Werner, O., Savic, V., Nagy, É., Czifra, G., and Lomniczi, B., 2003, Phylogenetic analysis reveals extensive evolution of avian paramyxovirus type 1 strains of pigeons (*Columba livia*) and suggests multiple species transmission: Virus Research, v. 96, p. 63–73.

van de Bildt, M.W., Kuiken, T., Visee, A.M., Lema, S., Fitzjohn, T.R., and Osterhaus, A.D., 2002, Distemper outbreak and its effect on African wild dog conservation: Emerging Infectious Diseases, v. 8, p. 211–213.

Vandevelde, M., Kristensen, B., Braund, K.G., Greene, C.E., Swango, L.J., and Hoerlein, B.F., 1980, Chronic canine distemper virus encephalitis in mature dogs: Veterinary Pathology, v. 17, p. 17–28.

Vandevelde, M., and Zurbriggen, A., 1995, The neurobiology of canine distemper virus infection: Veterinary Microbiology, v. 44, p. 271–280.

Van Kampen, K.R., 2001, Recombinant vaccine technology in veterinary medicine: Veterinary Clinics of North America, Small Animal Practice, v. 31, p. 535–538.

Verlaeten, O., Griffond, B., Khuth, S.T., Giraudon, P., Akaoka, H., Belin, M.F., Fellmann, D., and Bernard, A., 2001, Down regulation of melanin concentrating hormone in virally induced obesity: Molecular and Cellular Endocrinology, v. 181, p. 207–219.

Vickers, T., Garcelon, D., Fritcher, D., and Christianson, M., 2004, Evaluation of an oral and food-based canarypox-vectored canine distemper vaccine in endangered Channel Island Foxes (*Urocyon littoralis*): American Association of Zoo Veterinarians, Annual Proceedings, p. 89–90.

Visser, I.K.G., van Bressem, M.F., van de Bildt, M.W.G., Groen, J., Orvell, C., Raga, J.A., and Osterhaus, A.D., 1993, Prevalence of morbilliviruses among pinniped and cetacean species: Reviews in Science and Technology, v. 12, p. 197–202.

Welter, J., Taylor, J., Tartaglia, J., Paoletti, E., and Stephensen, C.B., 1999, Mucosal vaccination with recombinant poxvirus vaccines protects ferrets against symptomatic CDV infection: Vaccine, v. 17, p. 308–318.

Welter, J., Taylor, J., Tartaglia, J., Paoletti, E., and Stephensen, C.B., 2000, Vaccination against canine distemper virus infection in infant ferrets with and without maternal antibody protection, using recombinant attenuated poxvirus vaccines: Journal of Virology, v. 74, p. 6358–6367.

Westover, K.M., and Hughes, A.L., 2001, Molecular evolution of viral F and matrix protein genes and phylogenetic relationships among the Paramyxoviridae: Molecular and Phylogenetic Evolution, v. 21, p. 128–134.

Williams, E., Anderson, S.L., Cavender, J., Lynn, C., List, C., Heran, C., and Appel, M.J.G., 1996, Vaccination of black-footed ferret (*Mustela nigripes*) × Siberian polecat (*M. eversmanni*) hybrids and domestic ferrets (*M. putorius furo*) against canine distemper: Journal of Wildlife Diseases, v. 32, p. 417–423.

Williams, E.S., Edwards, J., Edwards, H., Welch, V., Dubay, S., Luce, B., and Anderson, S., 1997, Survey of coyotes for disease in Shirley Basin, Wyoming in 1996, *in* Luce, B., Oakleaf, B., and Williams, E.S., eds., Black-footed ferret reintroduction, Shirley Basin, Wyoming, 1996 annual completion report: Cheyenne, Wyoming Game and Fish Department, p. 34–43.

Williams, E.S., and Thorne, E.T., 1996, Infectious and parasitic diseases of captive carnivores, with special emphasis on the black-footed ferret (*Mustela nigripes*): Reviews in Science and Technology, v. 15, p. 91–114.

Williams, E.S., Thorne, E.T., Appel, M.J., and Belitsky, D.W., 1988, Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming: Journal of Wildlife Diseases, v. 24, p. 385–398.

Wimsatt, J., Biggins, D., Innes, K., Taylor, B., and Garell, D., 2003, Evaluation of oral and subcutaneous delivery of an experimental canarypox recombinant canine distemper vaccine in the Siberian polecat (*Mustela eversmanni*): Journal of Zoo and Wildlife Medicine, v. 34, p. 25–35.

Wimsatt, J., Jay, M.T., Innes, K.E., Jessen, M., and Collins, J.K., 2001, Serologic evaluation, efficacy, and safety of a commercial modified-live canine distemper vaccine in domestic ferrets: American Journal of Veterinary Research, v. 62, p. 736–740.

Wisely, S.M., Buskirk, S.W., Fleming, M.A., McDonald, D.B., and Ostrander, E.A., 2002, Genetic diversity and fitness in black-footed ferrets before and during a bottleneck: Journal of Heredity, v. 93, p. 231–237.

Woolhouse, M.E., Taylor, L.H., and Haydon, D.T., 2001, Population biology of multihost pathogens: Science, v. 292, p. 1109–1112.

Wunschmann, A., Kremmer, E., and Baumgartner, W., 2000., Phenotypical characterization of T and B cell areas in lymphoid tissues of dogs with spontaneous distemper: Veterinary Immunology and Immunopathology, v. 73, p. 83–98.


Heather Bramel
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Section VII. Extended Abstracts

The contributions contained in this section were presented at an evening poster session of the symposium.

Identifying Focal Areas for Conservation of Black-footed Ferrets and Prairie Dog Associates

By Jonathan Proctor,[1,2] Bill Haskins,[3] and Steve Forrest[4]

Introduction

Restoring viable populations of black-footed ferrets (*Mustela nigripes*) requires first restoring large complexes of prairie dog (*Cynomys* spp.) colonies. Ferret restoration within the former range of the black-tailed prairie dog (*C. ludovicianus*) requires prairie dog complexes of 4,000 ha or more (Conservation Breeding Specialist Group, 2004). Areas large enough to accommodate prairie dog complexes of this size may not be readily apparent from mapping the current distribution of prairie dogs alone. Remaining prairie dog colony distribution today is in large part an artifact of historical land use rather than habitat suitability or other biotic factors (e.g., Lomolino and Smith, 2003). Moreover, as a result of intensive control efforts, disease, and other management activities, few prairie dog complexes of this size exist in situ today. Necessarily, black-footed ferret recovery will therefore require expansion of prairie dogs into potential habitat, prairie dog translocations, and other “habitat-building” activities. Locating priority opportunities for ferret recovery will involve looking at both biogeographic criteria as well as socioeconomic constraints and concerns. Locating a suite of “restorable” landscapes, based on a coarse set of criteria that account for biological habitat suitability, land tenure, land management, contiguous size, and geographic representation, is a first step in this process (Forrest and others, 2004; Proctor and others, 2006). We used a geographic information system (GIS) to identify areas with restoration potential for the black-footed ferret within the former range of the black-tailed prairie dog, a species for which there are existing models of habitat suitability (e.g., Proctor, 1998).

Methods

We identified potential black-tailed prairie dog habitat within its former range by overlaying a grid of 90 × 90-m pixels on current U.S. Geological Survey vegetation maps (U.S. Geological Survey, 2000). Pixels were considered potential habitat if they contained vegetation classified as grasslands, grassland/herbaceous, shrublands, or transitional areas, removing from consideration all pixels with slopes >10 percent, in cropland, or in the Sandhills region of Nebraska (Proctor and others, 2006).

From this potential prairie dog habitat subset, we selected focal areas for conservation of black-footed ferrets in the following manner. On public lands, we identified as focal areas all contiguous potential prairie dog habitat of 20,000 ha or more. On tribal lands where ownership data were available (Montana and New Mexico), we identified the largest block of potential prairie dog habitat on each reservation with a minimum area of potential habitat >4,000 ha. Where ownership data for tribal lands were unavailable (e.g., the Dakotas and Nebraska), we simply indicated the existence of known large prairie dog complexes (e.g., the Rosebud, Pine Ridge, and Cheyenne River Reservations in South Dakota). We then identified all blocks of potential habitat >4,000 ha located on private reserves (e.g., owned by the Turner Endangered Species Fund or The Nature Conservancy). We placed circles roughly equal to the size of the potential habitat block over the midpoint of each focal area. Circles are meant to identify the general location as opposed to exact boundaries.

The results provided good geographic representation for most states and provinces. However, six States (Kansas, Nebraska, North Dakota, Oklahoma, Texas, Wyoming) contained fewer than five focal areas. In these States, we went below the 20,000-ha cutoff to identify the next largest focal areas on public lands so that each State had at least five focal areas. Finally, because Kansas still had only three focal areas due to limited ownership in public lands or key private lands, we identified an additional two blocks of potential habitat from private lands by iteratively removing the smaller aggregations of potential habitat until only the largest two blocks remained.

In areas where accurate prairie dog location data are available, it may also be possible to develop more robust

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conservation strategies based on “reserve design” concepts (Noss and others, 1999). Using Montana as an example, we identified core conservation areas for prairie dogs and associates, linkage habitat, and matrix habitat by scoring each 90 × 90-m pixel in Montana as follows: 1 if it was classified as potential black-tailed prairie dog habitat, else 0; 1 if it was within a current prairie dog colony (as mapped between 1988 and 2003 and defined by a 0.75-km buffer), else 0; 1 if it was within a block of potential habitat >4,000 ha on public land, tribal land, or a private reserve, else 0; and proximity to other prairie dog colonies, expressed as a value between 0 (at >24 km from a colony) and 1 (on a colony). The final score for each pixel was the total of the individual scores for these four criteria.

Results and Discussion

Using the methodology described, 92 focal areas for potential black-footed ferret recovery were identified (fig. 1). Of the areas identified, five contain seven separate ongoing ferret reintroduction programs; one had ferrets reintroduced, but they no longer survive; and eight have been identified through other processes as having reintroduction potential or are in the process of developing reintroduction programs. Thus, all current or proposed ferret reintroduction sites in the black-tailed prairie dog range were captured by this methodology. While inclusion of all of the current or proposed reintroduction sites provides some validation of the model used here, it also suggests that the most obvious or most readily restorable sites have already been identified and/or are in use. The remaining sites may be progressively more challenging in terms of their restoration potential either because of the lack of currently existing large prairie dog complexes or because of other factors such as resistance to endangered species reintroduction programs.

For Montana, development of a reserve design for ferrets based on multiple attributes is feasible (fig. 2) but also points to limited opportunities for large-scale restoration at multiple sites given current black-tailed prairie dog distribution.

While we limited this analysis to black-tailed prairie dog habitat, data exist to identify black-footed ferret recovery focal areas for both white-tailed (*C. leucurus*) and Gunnison’s (*C. gunnisoni*) prairie dogs as well. Recent assessments of those two species’ ranges suggest that good opportunities may exist in several locations beyond the four sites where recovery activities for ferrets are underway on white-tailed and Gunnison’s prairie dog range (Seglund and others, 2005a,b). A comprehensive, rangewide strategy for ferret recovery should incorporate these and other data to map out a path for the future of the species.

References Cited

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management planning workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

Forrest, S.C., Strand, H., Haskins, W.H., Reese, C., Proctor, J., and Dinerstein, E., 2004, Ocean of grass—a conservation assessment for the Northern Great Plains: Bozeman, Mont., Northern Plains Conservation Network and Northern Great Plains Ecoregion Program, World Wildlife Fund–U.S., http://worldwildlife.org/wildplaces/ngp/pubs/ocean-of-grass.cfm.

Lomolino, M.V., and Smith, G.A., 2003, Prairie dog towns as islands—applications of island biogeography and landscape ecology for conserving nonvolant terrestrial vertebrates: Global Ecology and Biogeography, v. 12, p. 275–286.

Noss, R.F., Dinerstein, E., Gilbert, B., Gilpin, M., Miller, G.J., Terborgh, J., and Trombulak, S., 1999, Core areas—where nature begins, *in* Terborgh, J., and Soulé, M., eds., Continental conservation—scientific foundations of regional reserve networks: Washington, D.C., Island Press, p. 99–128.

Proctor, J.D., 1998, A GIS model for identifying potential black-tailed prairie dog habitat in the Northern Great Plains shortgrass prairie: Missoula, University of Montana, M.S. thesis, 54 p.

Proctor, J., Haskins, B., and Forrest, S.C., 2006, Focal areas for conservation of prairie dogs and the grassland ecosystem, *in* Hoogland, J.L., ed., Conservation of the black-tailed prairie dog: Washington, D.C., Island Press, p. 232–247.

Seglund, A.E., Ernst, A.E., Grenier, M., Luce, B., Puchniak, A., and Schnurr, P., 2005a, White-tailed prairie dog conservation assessment: Laramie, Wyo., Western Association of Fish and Wildlife Agencies, 138 p.

Seglund, A.E., Ernst, A.E., and O’Neill, D.M., 2005b, Gunnison’s prairie dog conservation assessment: Laramie, Wyo., Western Association of Fish and Wildlife Agencies, 87 p.

U.S. Geological Survey, 2000, National land cover data: EROS Data Center, Sioux Falls, South Dakota.

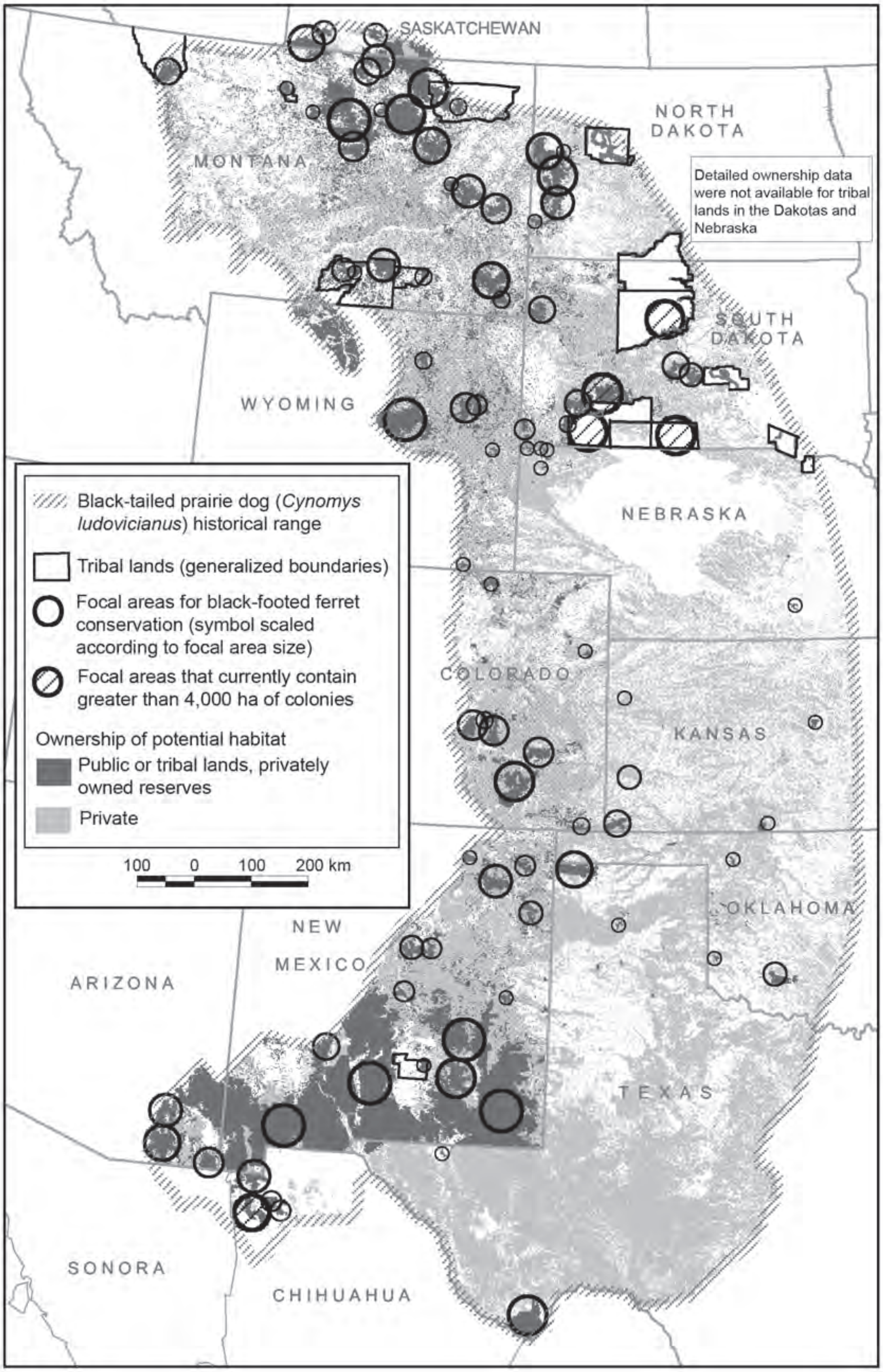

Figure 1. Focal areas for black-footed ferret (*Mustela nigripes*) recovery based on habitat suitability, land tenure, and public land contiguity.

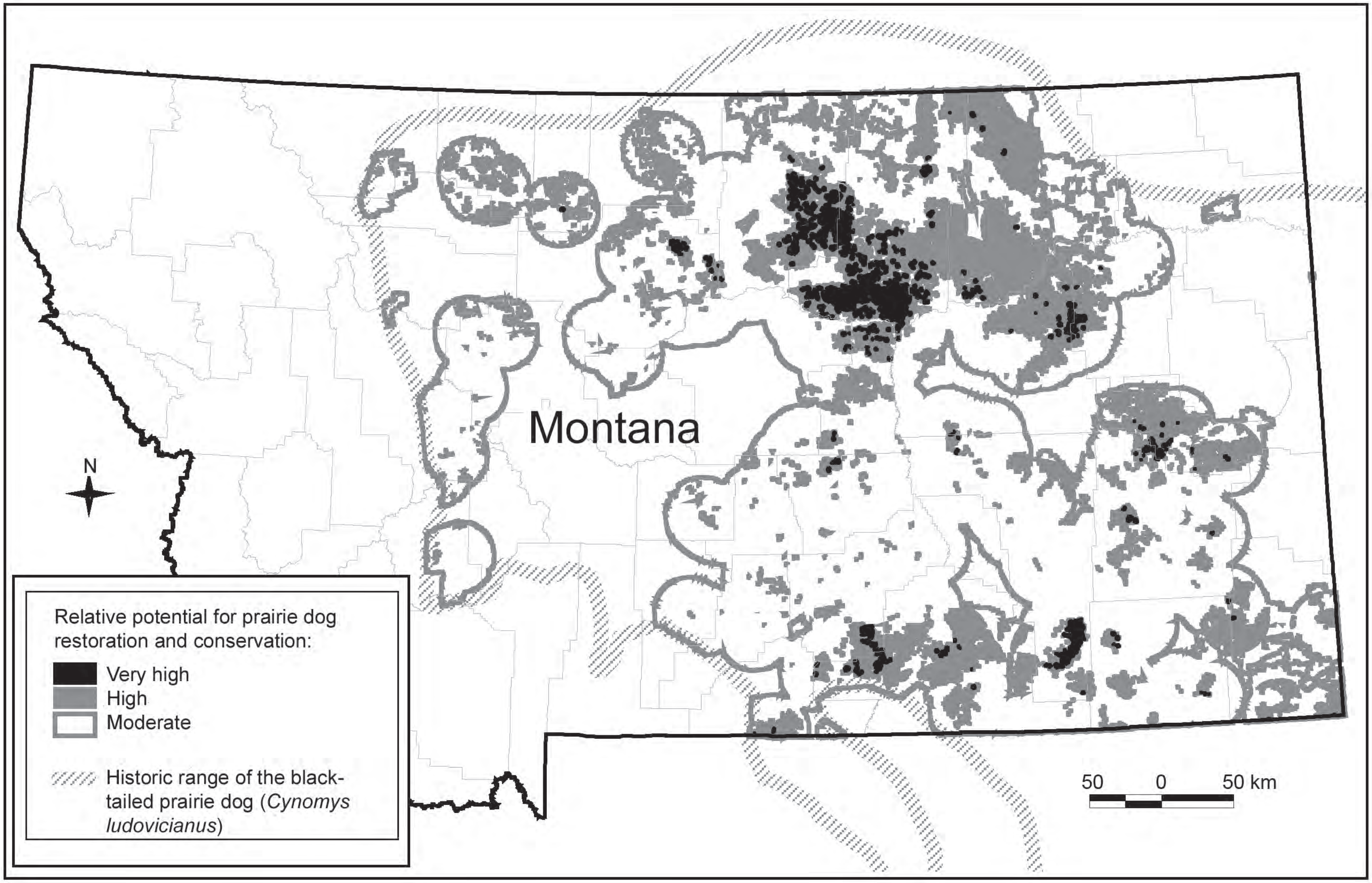

Figure 2. Relative potential for black-footed ferret (*Mustela nigripes*) recovery and restoration in Montana based on scores derived from habitat suitability, land ownership, and existing prairie dog (*Cynomys* spp.) distribution and abundance (moderate score = 1.0–2.0, high = 2.0–3.0, very high = 3.0–4.0).

White-tailed Prairie Dog Population Survey and Habitat Evaluation in Western Wyoming

By John A. Baroch[1,2] and David A. Plume[3]

Introduction

This study was conducted in the Pinedale Anticline Lease Area (PALA) of the Pinedale Field Office administrative unit of the U.S. Bureau of Land Management, Wyoming. The PALA and the adjacent Jonah II Lease Area (J2LA) contain large reserves of natural gas (Lyon and Anderson, 2003) and are sites of rapid energy exploration and extraction activities. The objectives of the study were to assess a variety of demographic variables and to provide a basis for linking prairie dog (*Cynomys* spp.) colonies to land features that might allow modeling of potential habitat. Recently compiled Global Positioning System (GPS) maps of white-tailed prairie dog (*C. leucurus*) colonies within the two mineral leases were available. These maps have been generated and updated annually for several years by a private contractor as part of an ongoing environmental assessment of the mineral leases. Approximately 30 colonies had been identified and mapped within the PALA in 2001. Twenty-nine of these colonies (hereafter referred to as the "base map colonies") were selected to study the demographics and habitat characteristics of white-tailed prairie dogs.

Study Area

The area consists of plains interspersed with isolated hills, plateaus, and low mountains. Elevation ranges from 1,800 to 2,400 m. Winters are cold and summers are short and hot. Average annual precipitation ranges from 130 to 360 mm and is fairly evenly distributed throughout the year. The vegetative community is classified as sagebrush steppe (Reid and others, 2002).

Methods

All burrows on 29 colonies were mapped by GPS in 2003 and classified as active or inactive. Active status was determined by the presence of fresh prairie dog scat in the opening or within 0.5 m of the opening. Fresh scat was defined as greenish, black, or dark brown in color and not dried hard or bleached white (Biggins and others, 1993).

Our survey concentrated on site factors that may influence the selection of white-tailed prairie dog burrows and colonies. Habitat characteristics were compared between the original colonies and nearby "ghost" polygons. The ghost polygons were computer-generated replicas of the actual colonies that were superimposed on the landscape at randomly chosen locations near each actual colony and within a range that was accessible to the prairie dogs (fig. 1).

Soil texture, soil depth, and ground cover were assessed on the colonies surveyed in 2001 and compared with samples from ghost colonies. Soil texture was assessed at a depth of

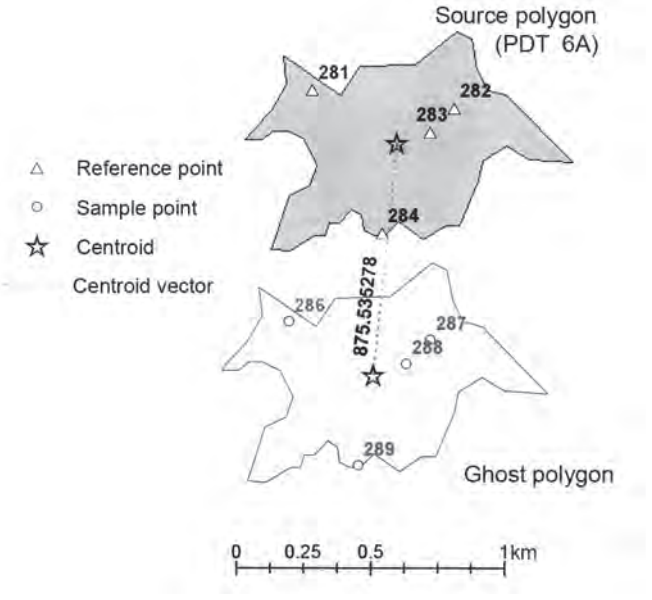

Figure 1. Generating ghost polygons and soil sample sites. Base map white-tailed prairie dog colony (*Cynomys leucurus*) PDT 6A is shown with the corresponding ghost polygon. The four soil survey sites, numbered 281–284, were selected using a randomization procedure applied to numbered cells overlaid on the source polygon. A second randomization algorithm selected the length and direction of the vector connecting the centroids. Soil survey points were projected along the same vector to locate ghost survey points that maintained the geometry of the source polygon.

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[3] Symmetry Corporation, P.O. Box 411, Niwot, CO 80544.

0.5 m. Samples were dried and sifted by particle size. Soil depth was defined as the maximum depth (up to 1 m) that could be reached with a hand driven, 8-cm diameter bucket auger. Ground cover and surface soil texture were assessed by the point-intercept survey method. The point-intercept method employs a sighting device or pin/point frame at selected sites to estimate the cover by type. Optical sighting devices eliminate observer bias when used properly since the sampling points are selected entirely by procedure. We fabricated an optical sighting device consisting of a vertical sighting tube with a peephole sight at the top end and an 8-cm diameter glass magnifying lens at the lower end. The sighting tube was attached to the end of a horizontal beam. When rotated 360° in a horizontal plane on a tripod, the optical sight described a circle 1 m in diameter. At each randomly selected sampling location, readings were made at 30° intervals. Cross hairs at the center of the magnifying lens pinpointed each sampling point.

Slope, aspect, and solar gain were derived from 10-m digital elevation model data and intersected with both colony areas and burrow point data. Colony slope and aspect were analyzed with circular statistical methods. The aspect of the 10 × 10-m cell containing each burrow recorded by the GPS was determined, and the results were sorted by active or inactive status.

Results and Discussion

The 2003 survey showed a dramatic reduction in the number of colonies since the earlier survey in 2001, with only 15 of 29 colonies surveyed still active. In terms of area, the active colonies in the vicinity of the 29 original colonies totaled just 71 ha. The original colonies composed 1,407 ha in 2001. Figure 2 illustrates one of the larger colonies that diminished in extent and population between 2001 and 2003. Of the 37 colonies mapped in 2003, 25 had what is considered a favorable or healthy ratio of active to inactive burrows (>1.0) (Biggins and others, 1993). Twelve colonies had ratios below 1.0. The mortality factors that threaten prairie dogs on a large scale include loss of habitat, urbanization, resource development, poisoning, recreational shooting, and sylvatic plague (caused by the bacterium *Yersinia pestis*) (Knowles, 2002). Information on the incidence and impact of plague in the study area is lacking.

Our comparison between the 2001 colonies and the randomly located ghost polygons did not find significant differences in soil depth (to 1 m) or in percent rocks in the soil profile at a depth of 0.5 m. We had hypothesized that variations in soil depth might affect site selection with regard to the ability to establish hibernacula below the frost line. We found soil depth to be at least 1 m throughout the surveyed areas. Since hibernacula are probably always deeper than 1 m, and we were not able to evaluate greater depths, we cannot draw any conclusions as to soil depth being a limiting factor.

The frequency distribution of mineral particle sizes on the surface was found to be almost identical between colonies and ghost polygons. However, there was nearly twice the amount of vegetative cover on colonies as opposed to ghost polygons. The significance of this observation in relation to prairie dog occupancy is unknown.

With respect to slope, aspect, and solar gain, we found that the mean angle and mean vectors were similar for all three sample sets (the base map colonies, ghost polygons, and currently active colonies). Mean angle of all polygons in the three groups was 160° on the base map colonies, 129° among the ghost polygons, and 121° among the currently active colonies. Mean vectors, which express the "evenness" of the dispersion of points around the compass, were 0.556, 0.446 and 0.492, for the base map colonies, ghost polygons, and active colonies, respectively. A value of 1.0 represents uniform dispersion of the vectors on a 360° circle.

The orientation of active and former colonies was found to be exclusively to the northeast, southeast, and southwest quarters of the compass. This orientation avoids the prevailing winds but may also be related to solar flux. Plots of the energy distribution of the entire landscape in the study area, when compared to the energy distribution of active burrow sites, provide evidence that the prairie dogs may be selecting sites within a range of solar gain that differs from expected levels.

We found the slope variation to be very similar in the 2001 colonies and the ghost polygons, but the slope variation on the currently occupied colonies was on average about half that of the other areas. This supports the hypothesis that evenness of slope may facilitate improved communications and predator detection (Wagner, 2002). It is unknown if the prairie

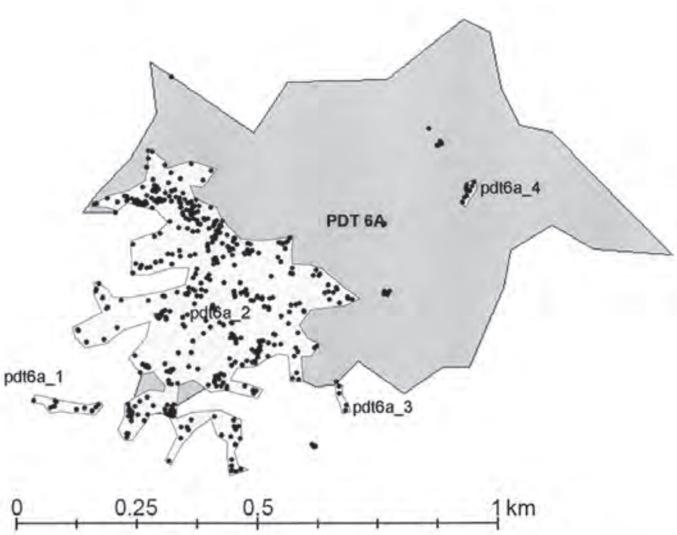

Figure 2. Trend toward fewer active burrows and contracting colony boundaries is illustrated by white-tailed prairie dog (*Cynomys leucurus*) colony PDT 6A. Active burrows recorded by GPS in early summer 2003, overlaid on the colony PDT 6A, mapped in 2001.

dogs preferentially select more even terrain, or if those occupying such terrain are more successful at avoiding predation.

A similar study of the Gunnison's prairie dog (*C. gunnisoni*) in Arizona was used to model habitat associations with the intent that the results might assist managers in estimating the suitability of unoccupied sites for possible prairie dog reintroduction (Wagner 2002). The results of our study may have similar applications for the white-tailed prairie dog.

References Cited

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood., A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Knowles, C., 2002, Status of white-tailed and Gunnison's prairie dogs: Missoula, Mont., National Wildlife Federation, and Washington, D.C., Environmental Defense Fund, 30 p.

Lyon, A.G., and Anderson, S.H., 2003, Potential gas development impacts on sage grouse nest initiation and movement: Wildlife Society Bulletin, v. 31, p. 486–491.

Reid, M., Comer, P., Barrett, H., Caicco, S., Crawford, R., Jean, C., Jones, G., Kagan, J., Karl, M., Kittel, G., Lyon, P., Manning, M., Peterson, E., Rosentreter, R., Rust, S., Tart, D., Williams, C., and Winward, A., 2002, International classification of ecological communities—terrestrial vegetation of the United States. Sagebrush vegetation of the Western United States: Arlington, Va., NatureServe, Final report for the U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Boise, Idaho, 23 p.

Wagner, D.M., 2002, Current status and habitat use of Gunnison's prairie dogs (*Cynomys gunnisoni*) in Arizona: Flagstaff, Northern Arizona University, Ph.D. dissertation, 77 p.

Can the Systemic Insecticide Nitenpyram Be Used for Flea Control on Black-tailed Prairie Dogs?

By Jeff N. Borchert[1] and Jeff J. Mach[1]

Introduction

Plague has the potential to decimate prairie dog (*Cynomys* spp.) populations and is a threat to reintroduction of the black-footed ferret (*Mustela nigripes*), which requires large colonies of prairie dogs for food (Biggins and Godbey, 2003). Controlling flea (Insecta: Siphonaptera) populations on prairie dogs at reintroduction sites could decrease the risk of plague. Currently, fleas in prairie dog towns are controlled by using permethrin or deltamethrin dust (Beard and others, 1992; Seery, 2003). However, these compounds may be detrimental to nontarget arthropods.

Systemic insecticides, commonly used for flea control in veterinary medicine, might be useful in controlling flea populations on prairie dogs, but little use has been made of such compounds added to rodent bait for control of plague (Gratz, 1999). Nitenpyram is an insecticide that has been used for the control of aphids, thrips, leafhoppers, whiteflies, and other suckling insects of rice and has also demonstrated effectiveness against the cat flea (*Ctenocephalides felis*) as a topical treatment (Tomlin, 2000; Moyses and Gfeller, 2001). Nitenpyram is also effective for systemic control of fleas on pets and is currently used in a commercial systemic flea treatment for dogs and cats called Capstar® (Novartis Animal Health, Greensboro, N.C.) (Rust and others, 2003). We investigated the efficacy of systemically delivered nitenpyram formulated at 560 mg/kg in rodent bait against a ground squirrel flea (*Oropsylla montana),* which readily transmits plague, on black-tailed prairie dogs (*C. ludovicianus*).

Methods

Prairie dogs were captured in Larimer County, Colo., transported to Genesis Laboratories, Inc., and acclimated to laboratory conditions for 13 days. Medicated prairie dog bait was prepared by mixing 20 Capstar tablets (56 mg nitenpyram/tablet) in palatable grains and powdered sugar (2 kg total). The medicated diet was presented to the prairie dogs for 48 hours. Food consumption was measured daily. Artificial flea feeding apparatuses were constructed with centrifuge tubes, 300 µm nylon mesh, and plumber's glue to allow fleas to feed without being lost. Four to six fleas (*O. montana*) obtained from the Genesis Laboratories breeding colony were added to each flea feeder. The apparatuses were secured to prairie dogs for 24 hours with athletic tape on an area of shaved fur. The apparatuses were then removed, and the fleas were immediately evaluated for mortality and morbidity by placing them in a large white plastic container. By blowing on the fleas, we could ascertain mortality or morbidity by the presence or absence of movement. The process was repeated on day 3 after exposure for evaluation of residual effect.

Results

Bait containing 560 mg/kg nitenpyram was effective at producing mortality and morbidity in fleas at day 1 (table 1) and minimally at day 3. Day 1 flea mortality was 76.9 percent. Of the 11 fleas surviving, 5 (45.5 percent) were observed to be moribund. Day 3 flea mortality was 23.1 percent. Of the 10 fleas surviving at day 3, 0 (0 percent) were observed to be moribund.

Discussion and Management Implications

Nitenpyram was initially effective at controlling *O. montana* fleas on black-tailed prairie dogs, causing greater than 70 percent mortality at day 1. Mortality of fleas declined to 23.1 percent by day 3. Observations in other ground squirrels (*Spermophilus* spp.) indicate that recolonization of hosts by fleas is very rapid, within 3 days (Ryckman, 1971). Because of the lack of residual action of systemically delivered nitenpyram, this compound would likely not be effective as a method of preventative plague control in prairie dogs. A systemically delivered insecticide with longer residual effect might be beneficial in a plague control program of this type.

In addition to their potential utility in controlling fleas on prairie dogs at black-footed ferret recovery sites, rodent baits containing insecticide might also be effective for preventative flea control in situations where rodents live close to humans,

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Table 1. The 24-hour efficacy of systemic nitenpyram on *Oropsylla montana* fed on black-tailed prairie dogs (*Cynomys ludovicianus*).

Prairie dog number	Sex	Active ingredient consumed (mg)	Body weight (kg)	Dose (mg/kg)	Number of fleas applied	Fleas dead/ fleas recovered	Fleas moribund/ fleas recovered alive
Treatment							
1	M	25.9	0.827	31.3	5	Not recovered	
3	M	35.3	0.475	74.3	4	3/4	0/1
4	F	4.0	0.798	5.0	4	1/4	1/3
6	M	29.3	0.924	31.7	5	5/5	-
7	M	12.4	0.895	13.9	5	5/5	-
8	M	21.8	1.109	19.7	5	4/5	1/1
9	M	38.9	1.175	33.1	6	6/6	-
11	F	2.3	0.710	3.2	5	2/5	0/3
12	M	42.0	1.111	37.8	5	5/5	-
14	F	24.7	0.773	32.0	4	2/4	1/1
15	M	23.4	1.225	19.1	4	3/4	1/1
16	F	27.9	0.964	28.9	5	4/5	1/1
Mean		24.0	0.916	27.5	Total	40/52 (76.9%)	5/11 (45.5%)
Control							
1	M	-	0.775	-	4	0/4	-
2	M	-	1.159	-	5	0/5	-
3	M	-	0.655	-	5	1/5	-
4	M	-	0.872	-	5	0/5	-
Mean		-	0.865	-	Total	1/19 (5.3%)	-

but other rodent control methods are not acceptable to the public. For example, the City of Fort Collins, Colo., maintains approximately 2,000 acres of active black-tailed prairie dog colonies within the Urban Growth Area. Lethal control of these prairie dogs has been a contentious issue among Fort Collins residents (City of Fort Collins, 1998). Baits incorporating insecticides might be ideal in such a situation as potential risk to humans would likely decrease and the prairie dogs themselves would not be harmed.

References Cited

Beard, M.L., Rose, S.T., Barnes, A.M., and Montenieri, J.A., 1992, Control of *Oropsylla hirsute*, a plague vector, by treatment of prairie dog burrows with 0.5% permethrin dust: Journal of Medical Entomology, v. 29, p. 25–29.

Biggins, D.E., and Godbey, J.L., 2003, Challenges to reestablishment of free-ranging populations of black-footed ferrets: Comptes Rendus Biologies, v. 326 (Suppl. 1), p. S104–S111.

City of Fort Collins, 1998, Prairie dog policies for natural areas: Fort Collins, Colo., Prairie Dog Review Committee, Natural Resources Department, 24 p.

Gratz, N.G., 1999, Control of plague transmission, *in* Plague manual: Geneva, Switzerland, World Health Organization, p. 97–134.

Moyses, E.W., and Gfeller, F.J., 2001, Topical application as a method for comparing the effectiveness of insecticides against cat flea (Siphonaptera: Pulicidae): Journal of Medical Entomology, v. 38, p. 193–196.

Rust, M.K., Waggoner, M.M., Hinkle, N.C., Stansfield, D., and Barnett, S., 2003, Efficacy and longevity of nitenpyram against adult cat fleas (Siphonaptera: Pulicidae): Journal of Medical Entomology, v. 40, p. 678–681.

Ryckman, R.E., 1971, Plague vector studies 3. The rate deparasitized ground squirrels are reinfested with fleas under field conditions: Journal of Medical Entomology, v. 8, p. 668–670.

Seery, D.B., Biggins, D.E., Montenieri, J.A., Enscore, R.E., Tanda, D.T., and Gage, K.L., 2003, Treatment of black-tailed prairie dog burrows with deltamethrin to control fleas (Insecta: Siphonaptera) and plague: Journal of Medical Entomology, v. 40, p. 718–722.

Tomlin, C.D.S., 2000, The pesticide manual: Farnham, U.K., British Crop Protection Council, 1,344 p.

Fleas and Small Mammal Hosts Within and Adjacent to the Coyote Basin White-tailed Prairie Dog Colony in Northeastern Utah

By Lianna K. Etchberger,[1] William E. Stroh,[2] Brent D. Bibles,[3] Matthew R. Dzialak,[1] and Richard C. Etchberger[1]

Introduction

The endangered black-footed ferret (*Mustela nigripes*) and its prairie dog (*Cynomys* spp.) prey are susceptible to sylvatic plague, an infectious disease caused by the bacterium *Yersinia pestis*. Plague is a contagious disease transmitted by bites of vector fleas (Insecta: Siphonaptera), consumption of infected tissue, or contact with infected animals. Epizootics of plague are a threat to prairie dog and ferret populations at most reintroduction sites due to high mortality rates of both ferrets and prairie dogs. While much effort is currently focused on protecting these species from plague by flea control and vaccine development, little is understood about the reservoirs of this disease in the wild. Contributions to this understanding will lend insight for designing plague monitoring and transmission prevention protocols and for any effort to expand habitat for black-footed ferrets and prairie dogs.

Factors influencing the occurrence of plague epizootics are not fully understood (reviewed in Gage and Kosoy, 2005). In the arid Southwest, for example, favorable climate conditions correlate with plague epizootics (Parmenter and others, 1999; Enscore, 2002). While other models exist, there is speculation that climate may correlate with epizootics through increased rodent host populations (Parmenter and others, 1999; Enscore and others, 2002; Stapp and others, 2004). High population density increases the likelihood of transmission of a contagious disease once the pathogen is introduced to the susceptible population (Madigan and others, 2000). Population growth can also lead to expansion into adjacent areas atypical of short grassland prairie dog habitat. Indeed, active and inactive burrows have been found in dense sagebrush and on hillsides in a white-tailed prairie dog (*C. leucurus*) colony in Coyote Basin in northeastern Utah (L. Etchberger, personal observation, 1999). White-tailed prairie dog expansion into new habitat may therefore result in increased exposure to one or more flea or small mammal host species that are more likely to transmit plague to the population. This increased exposure may be caused by either overlapping ranges between the prairie dogs and flea vector or reservoir host or by expansion into an area with increased frequency of either the vector or the reservoir. While different flea species have different biological transmission rates in laboratory settings, mechanical transmission has also been observed (reviewed in Gage and Kosoy, 2005), suggesting that most flea species may be potential candidates for transmission in the wild. In this study, we present preliminary analyses of data comparing small mammal hosts and their flea species collected from white-tailed prairie dog habitat to those collected from adjacent habitat with the potential for prairie dog expansion. Patterns of flea species associations with host or habitat may help identify potential plague reservoirs.

Methods

We used field data on prairie dog distribution in Coyote Basin, Utah, and a geographic information system (ArcView®; Environmental Systems Research Institute, Inc., Redlands, Calif.) to delineate habitat occupied by white-tailed prairie dogs (PD) and adjacent habitat that was not occupied by prairie dogs (NOPD). Occupied habitat included a 50-m buffer adjacent to the colony perimeter; all habitat delineated as NOPD was at least 50 m from the colony boundary. We established small mammal trapping grids within PD and NOPD areas. To select specific grid locations, we used ArcView to generate 20 random points in each area, and we surveyed these locations systematically. Upon identifying a location in each area that we considered appropriate logistically, we selected that location as the southwest corner of a trapping grid. Grids consisted of 100 Sherman live traps placed 10 m apart in a 10 × 10 array. Grids were revisited for two to four trapping

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sessions each summer. Small mammals were trapped for two consecutive nights on the four grids (800 trap nights) during each session. Animals trapped on the second night were processed by determining weight and sex and combing for fleas after anesthesia with isoflurane. We restricted processing to animals trapped on the second night to facilitate objectives of additional research not presented here. Fleas were collected in a tube with saline/Tween detergent solution, pooled for each individual host animal, and sent to the Bacterial Zoonoses Branch, Centers for Disease Control and Prevention (CDC) in Fort Collins, Colo., for species identification. We used Fisher's exact test to evaluate differences in the occurrence of small mammal species, flea species, or flea host species distributed between PD and NOPD habitats. Significance was set at $P \leq 0.05$.

Results

A preliminary analysis of pooled data collected between the years 2000 and 2004 is reported here. Spatial and temporal analyses will be reported elsewhere.

Small mammal species and their distribution between the PD and NOPD locations are shown in table 1. The majority (96 percent) of small mammals trapped were deer mice (*Peromyscus maniculatus*). We also trapped Ord's kangaroo rats (*Dipodomys ordii*) and piñon mice (*P. truei*) along with one northern grasshopper mouse (*Onychomys leucogaster*) and one thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). Of the 822 small mammals trapped, 405 were trapped in PD grids and 417 were trapped in NOPD grids. Differences in the occurrence of small mammal species between PD and NOPD habitats were significant ($P = 0.04$), largely reflecting the differences in abundance of Ord's kangaroo rats between sites.

Table 1. Distribution of small mammals and fleas from habitats occupied (PD) and not occupied (NOPD) by white-tailed prairie dogs (*Cynomys leucurus*).

	PD	NOPD	Species total
Small mammals			
Deer mouse (*Peromyscus maniculatus*)	396	396	792
Ord's kangaroo rat (*Dipodomys ordii*)	5	17	22
Piñon mouse (*P. truei*)	3	3	6
Northern grasshopper mouse (*Onychomys leucogaster*)	1	0	1
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	0	1	1
Total	405	417	822
Fleas			
Aetheca wagneri	136	122	258
Meringus sp.	2	17	19
Epitidea wemmani	2	10	12
Amaradix euphorbi	5	3	8
Orchopeas sexdentatus	0	2	2
Total	145	154	299

Flea species and their distribution between the PD and NOPD locations are shown in table 1. The majority (86 percent) of fleas collected were *Aetheca wagneri*; *Meringus* sp., *Epitidea wemmani*, *Amaradix euphorbi*, and *Orchopeas sexdentatus* were also collected. There was some concern at the CDC as to whether the *O. sexdentatus* identification was correct because this species is not normally associated with the deer mouse host on which it was found. Of the 299 fleas collected, 145 were collected from small mammal hosts trapped in PD grids, and 154 were from NOPD grids. The difference in the occurrence of flea species between PD and NOPD habitats was significant ($P < 0.01$), reflecting the increased occurrence of *Meringus* sp. and *E. wemmani* in NOPD locations.

All fleas collected were from deer mice and Ord's kangaroo rats. The flea/host relationships and distributions are shown in table 2. Numbers represent host species infested with each flea species. The majority of infested hosts were deer mice with *A. wagneri* fleas. There was no statistical difference in the flea/host relationships between the PD and NOPD habitats; the occurrence of deer mice, Ord's kangaroo rats, and total number of hosts infested with various flea species did not vary between the two habitats ($P = 0.27$, 0.29, and 0.44, respectively).

Discussion

Small mammals and their fleas were collected in the white-tailed prairie dog colony of Coyote Basin, Utah, for the

Table 2. Numbers of small mammals infested with fleas from habitats occupied (PD) and not occupied (NOPD) by white-tailed prairie dogs (*Cynomys leucurus*).

	Deer mouse (*Peromyscus maniculatus*)			Ord's kangaroo rat (*Dipodomys ordii*)		
	PD	NOPD	Total	PD	NOPD	Total
Aetheca wagneri	70	63	133	1	0	1
Meringus sp.	1	1	2	1	5	6
Epitidea wemmani	2	7	9	0	0	0
Amaradix euphorbi	2	1	3	0	0	0
Orchopeas sexdentatus	0	1	1	0	0	0
Total infested hosts	75	73	148	2	5	7

past five seasons. By returning to the same grid locations every year in this ongoing study, we have boosted our small sample sizes to better detect patterns in species composition and abundance. By comparison to prairie dog-occupied habitat, we observed that Ord's kangaroo rats and *E. wemmani* and *Meringus* sp. fleas were more abundant outside the colony boundary. Whereas deer mice were equally distributed, those infested with *E. wemmani* occurred more often in habitat outside of the colony. Also, *Meringus* sp. was found on both deer mice and Ord's kangaroo rats, an interesting observation since many flea species associate with only one host species. The preliminary observation that these flea and host species occur more frequently outside but near the Coyote Basin white-tailed prairie dog colony may have implications in plague transmission to prairie dogs and black-footed ferrets from an unidentified reservoir.

References Cited

Enscore, R.E., Biggerstaff, B.J., Brown, T.L., Fulgham, R.F., Reynolds, P.J., Engelthaler, D.M., Levy, C.E., Parmenter, R.R., Montenieri, J.A., Cheek, J.E., Grinnell, R.K., Ettestad, P.J., and Gage, K.L., 2002, Modeling relationships between climate and the frequency of human plague cases in the southwestern United States, 1960–1997: American Journal of Tropical Medicine and Hygiene, v. 66, p. 186–196.

Gage, K.L., and Kosoy, M.Y., 2005, Natural history of plague—perspectives from more than a century of research: Annual Review of Entomology, v. 50, p. 505–528.

Madigan, M.T., Martinko, J.M., and Parker, J., 2000, Brock biology of microorganisms (9th ed.): Upper Saddle River, N.J., Prentice-Hall, Inc., 991 p.

Parmenter, R.R., Yadav, E.P., Parmenter, C.A., Ettestad, P., and Gage, K.L., 1999, Incidence of plague associated with increased winter-spring precipitation in New Mexico: American Journal of Tropical Medicine and Hygiene, v. 61, p. 814–821.

Stapp, P., Antolin, M.F., and Ball, M., 2004, Patterns of extinction in prairie dog metapopulations—plague outbreaks follow El Niño events: Frontiers in Ecology and the Environment, v. 2, p. 235–240.

Effects of Moonlight on Cover Usage and Spatial Learning of Black-footed Ferrets

By Samantha N. Marcum,[1,2] Dean E. Biggins,[3] and Jennifer A. Clarke[1]

Conservation biology and animal behavior are two fields of science that can complement one another. Animal behavior research is important for understanding the complex needs of a species to be managed or restored to its native range and can be a critical part of the foundation for preservation of a species. Black-footed ferrets (*Mustela nigripes*) are endangered, nocturnal carnivores native to the North American prairie ecosystem. Siberian polecats (*M. eversmannii*) are their closest living relative and inhabit the steppe grasslands of Asia and Eastern Europe. Polecats were used as a surrogate species for behavioral studies in the initial stages of restoration attempts for the black-footed ferret. In previous studies, ferrets and polecats were highly susceptible to predation (Biggins, 2000). In this study, we hypothesized that ferrets and polecats would react to moonlight similarly to small nocturnal mammalian prey species that decrease activity and increase use of cover with increasing moonlight to avoid predation (Kavanau, 1969; Clarke, 1983; Falkenberg and Clarke, 1998; Zollner and Lima, 1999). We investigated the effects of moonlight on nocturnal cover usage and spatial learning abilities of black-footed ferrets. Multivariate general linear models with a repeated measures design were used to analyze data with $P = 0.05$ chosen as the significance level.

We tested cover usage by black-footed ferrets ($n = 8$) in an indoor chamber (7 m^2) under simulated new (0.05 lux), half (0.35 lux), and full (2.2 lux) moonlight levels. We measured use of cover (edge, burrows) and open areas. We detected no effect of moonlight level on use of cover versus open space for black-footed ferrets. Free-ranging ferrets and polecats studied previously increased their aboveground activity and movements with increasing moonlight levels, and black-footed ferret activity was low during primary activity periods of their principal predators, regardless of moonlight levels (Biggins, 2000). Energetic demands of ferrets may not allow moonlight to be a principal determinant of activity even if they prefer certain light levels. Also, light may be beneficial for spatial learning of home ranges, finding burrows, and locating prey or mates.

Spatial learning refers to the ability to remember the location of key features in one's environment (Gaulin and Fitzgerald, 1989; Lavenex and Schenk, 1998). Ferrets may use moonlight to examine their surroundings. We tested black-footed ferret spatial learning abilities (as indexed by distance traveled before the subject found a goal in a faux burrow) in a hexagonal indoor chamber (9 m^2) in new, half, and full moonlight levels. The ferrets typically stayed close to the walls of the arena during trials, a behavior known as thigmotaxy. Black-footed ferrets seemed to learn, but moonlight levels appeared to have no effect on that process. Polecats tested in another study that used similar methods (Sheffer, 2001) exhibited spatial learning abilities that appeared to be enhanced in half moonlight. Black-footed ferrets may be more nocturnally adapted than polecats (Biggins, 2000; Sheffer, 2001). Both species traveled less with successive spatial learning trials, suggesting that they either learned the goal location or the ritual for the test (fig. 1). Black-footed ferrets did not decrease the distance traveled to locate the goal in full moonlight; there was no evidence for a positive correlation between spatial learning and light level. Overall, black-footed ferrets traveled shorter distances than did polecats (fig. 1). Learning abilities of both species should be examined further to determine how cage rearing might affect spatial learning skills (e.g., Biggins and others, 1998). If these skills can be lost or fail

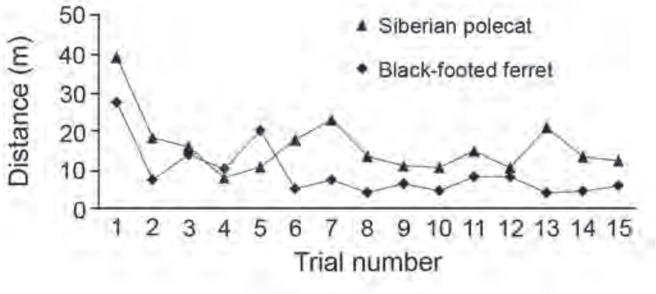

Figure 1. Mean distance traveled (m) by black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*) during 15 consecutive trials.

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to develop without appropriate stimuli, then modifications in captive breeding facilities may be necessary. Understanding these aspects of ferret behavior may be critical to conservation efforts for the species, particularly the success of captive breeding programs and species restoration. For example, better understanding of ferret behaviors under varying light levels may lead to increased efficiency in searching for ferrets (Biggins, Godbey, Matchett, and others, this volume) and improved interpretations of both energetic relationships (Harrington and others, this volume) and interactions with other predators (Breck and others, this volume).

References Cited

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Clarke, J.A., 1983, Moonlight's influence of predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*): Behavioral Ecology and Sociobiology, v. 13, p. 205–209.

Falkenberg, J.C., and Clarke, J.A., 1998, Microhabitat use of deer mice: effects of inter-specific interaction risks*:* Journal of Mammalogy, v. 79, p. 558–565.

Gaulin, S., and Fitzgerald, R., 1989, Sexual selection for spatial-learning ability: Animal Behaviour, v. 37, p. 322–331.

Kavanau, J.L., 1969, Influences of light on activity of small mammals: Ecology, v. 50, p. 548–557.

Lavenex, P., and Schenk, F., 1998, Olfactory traces and spatial learning in rats: Animal Behaviour, v. 56, p. 1129–1136.

Sheffer, K.H., 2001, The effect of moonlight on spatial learning in steppe ferrets: Greeley, University of Northern Colorado, M.S. thesis, 48 p.

Zollner, P.A., and Lima, S.L., 1999, Illumination and the perception of remote habitat patches by white-footed mice: Animal Behaviour, v. 58, p. 489–500.

Modeling Black-footed Ferret Energetics: Are Southern Release Sites Better?

By Lauren A. Harrington,[1,2] Dean E. Biggins,[3] and A. William Alldredge[1]

Introduction

Several models have been developed to estimate prey requirements and to assess habitat suitability of release sites for the black-footed ferret (*Mustela nigripes*) (e.g., Stromberg and others, 1983; Powell and others, 1985; Biggins and others, 1993). None of these models, however, addressed possible differences in energetic requirements between sites due to climatic differences within the ferret's historical range. We used a simplified energetics model to examine the effect of variation in environmental conditions on ferret energetic requirements. The aim of the study was to determine whether the ferret might be more successful in one area than another.

The Model

The total daily energy expenditure (E_{DEE}) of any mammal can be conceptualized as the sum of all mutually exclusive sources of energy expenditure (E_x) (Wunder, 1975; Powell and others, 1985). For a nonreproductive, fully grown adult, E_{DEE} can be modeled in the general form:

$$E_{DEE} = E_s + E_a + E_t$$

where E_s is the energy cost of resting; E_a is the energy cost of activity, including, in this case, running (E_r), digging (E_d), and standing (E_{st}) (Powell and others, 1985); and E_t is the energy cost of thermoregulation. We included thermoregulatory costs below the animal's lower critical temperature (T_{LC}) only and divided this into the cost above ground (E_{ta}) and below ground (E_{tu}). The inclusion of thermoregulation in the model was conditional upon Ta input. We estimated the total energy requirements of the animal for one day (in kJ) as:

$$E_{DEE} = E_s + E_r + E_d + E_{st} + [\text{if } Ta_a < T_{LC}]\ E_{ta} + [\text{if } Ta_u < T_{LC}]\ E_{tu}$$

where E_i is estimated as M_i x t_i (M_i is the energetic cost of activity i in kJ per hour; t_i is the time spent in activity i in hours per day), Ta_a is the ambient temperature above ground, and Ta_u is the temperature within the burrow (details in Harrington, 2001).

Model parameter estimates were from the literature, with empirical data on black-footed ferret metabolism from Harrington (2001) and Harrington and others (2003) and site temperature data (Ta_a) from meteorological records.

Model Simulations

For three hypothetical sites in the extreme north, south, and middle of the ferret's historical range, the model was run for 11 different activity scenarios ranging from complete rest within burrows to 5 hours active above ground (activity data from Powell and others, 1985). For each model run, Ta_a was chosen at random from a hypothesized normal distribution approximating nighttime temperature for each site in summer and winter. Ta_u was chosen at random from a range of values from the literature for summer and winter (same for all sites). Means and variances were based on 100 runs of the model for each of the 11 activity scenarios, for each site, in winter and summer.

Results

Assuming all activity scenarios are carried out at all sites in winter and summer, the model predicted higher energy requirements in the north than in the south in winter. In summer, energy requirements were predicted to be lower in the south than in the middle of the ferret's range. All other comparisons were nonsignificant. In all cases, variability within a site and season was high due to the inclusion of all possible activity scenarios in the simulations. Separating the analysis into low, medium, and high activity levels revealed that although trends tended to be similar (higher in the north than in the south), differences between sites were greatest at high activity levels and during winter. For resting ferrets, no differences between sites were detected; this was, however, an artifact of the model resulting from the use of a constant value

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for Ta_u. If burrow temperatures do vary between sites, overall intersite differences are likely to be greater.

Discussion

Although our model predicted statistically significant differences in energy requirements between northern and southern sites, these differences were small (<100 kJ per day between sites or about 11 percent of total mean expenditure during winter) and would require only small increases in prey consumption (one black-tailed prairie dog [*Cynomys ludovicianus*], the ferret's main prey, provides between 4,000 and 5,000 metabolizable kJ of energy; Powell and others, 1985). More biologically meaningful differences were found in consideration of energetic limits.

If maximum sustained metabolic rates for ferrets are limited at five times the basal metabolic rate (as they are for most other animals; Hammond and Diamond, 1997), maximum daily energy expenditure may be limited to approximately 1200 kJ per day, or less. Plotting predicted energy required per day in relation to above ground temperature demonstrated that, on this basis, high activity levels may be prohibitive at temperatures below -35°C (fig. 1). Although ferrets have been observed above ground at temperatures as low as -40°C (Richardson and others, 1987), it is not known how long they can stay above ground at such extremes. Ferret movements are shorter in colder temperatures; on the coldest days, ferrets simply may not be able to remain above ground. Ferret movements in late winter are principally for mating (Richardson and others, 1987); thus, restricted activity at this time could adversely affect reproductive potential.

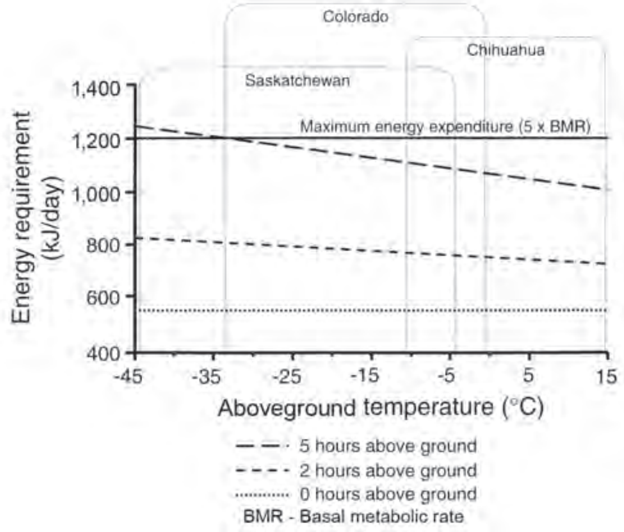

Figure 1. Predicted daily energy requirements for a black-footed ferret (*Mustela nigripes*) in winter in relation to aboveground temperature and amount of time spent above ground. Bracketing lines depict the range of winter temperatures for example sites. Activity was modeled to include mostly running with some time spent standing; Ta_u was set at 7.5°C (midpoint of the winter range).

Management Implications and Questions Remaining

This study does not provide definitive answers regarding the effect of climatic variability on ferret energy requirements. It does suggest, however, that ferret energetics and climate may be important factors to consider in evaluating potential release sites. If ferrets are to be successfully reintroduced into the wild, management plans should seek to minimize sources of stress to the extent possible. Winter energy requirements may be reduced by selecting more southerly reintroduction sites. As with all models, our predictions will require field validation. Questions remaining include (but are not limited to) the following. Is water stress greater in the south? How much do burrow temperatures vary between sites (and can ferrets manipulate their own burrow temperature by selecting depth)? How does ferret activity vary throughout their range (and in response to climate)?

References Cited

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Hammond, K.A., and Diamond, J., 1997, Maximal sustained energy budgets in humans and animals: Nature, v. 386, p. 457–462.

Harrington, L.A., 2001, Application of an energetics model to evaluate release-site potential for the black-footed ferret (*Mustela nigripes*): Fort Collins, Colorado State University, M.S. thesis, 126 p.

Harrington, L.A., Biggins, D.E., and Alldredge, A.W., 2003, Basal metabolism of the black-footed ferret (*Mustela nigripes*) and the Siberian polecat (*M. eversmannii*): Journal of Mammalogy, v. 84, p. 497–504.

Powell, R.A., Clark, T.W., Richardson, L., and Forrest, S.C., 1985, Black-footed ferret *Mustela nigripes* energy expenditure and prey requirements: Biological Conservation, v. 34, p. 1–15.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets

(*Mustela nigripes*) at Meeteetse, Wyoming: American Midland Naturalist, v. 117, p. 225–239.

Stromberg, M.R., Rayburn, R.L., and Clark, T.W., 1983, Black-footed ferret prey requirements—an energy balance estimate: Journal of Wildlife Management, v. 47, p. 67–73.

Wunder, B., 1975, A model for estimating metabolic rate of active or resting mammals: Journal of Theoretical Biology, v. 49, p. 345–354.

Roelle and others, eds.—**Recovery of the Black-footed Ferret: Progress and Continuing Challenges**—U.S. Geological Survey Scientific Investigations Report 2005-5293

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Black-tailed Prairie Dog Interstate Coordinator
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Rock Springs, Wyoming 82901

Dear Bob:

Pursuant to a request you made at the Black-footed Ferret Recovery Implementation Team (BFFRIT), Executive Committee meeting in Phoenix last December, I am writing to provide you with information on black-footed ferret (ferret) habitat needs and recovery direction. Such information is pertinent given current interstate black-tailed prairie dog conservation planning efforts, and it is important that prairie dog and ferret management strategies are closely coordinated. Indeed, the U.S. Fish and Wildlife Service (Service) must ensure, through Endangered Species Act section 7 consultation processes, that candidate conservation agreements for black-tailed prairie dogs are developed in a manner that will not foreclose, or appreciably impact, black-footed ferret recovery potential.

As you are aware, the black-footed ferret is one of the most endangered mammals in North America. It is an obligate of three prairie dog species, over which their respective historical ranges closely overlap. Given the specialized dependence of the ferret on prairie dogs, both the ferret's decline and ultimate recovery has been/is tied to prairie dog population stability and habitat quality. Although this principle has always been understood, ferret recovery partners have focused much of their past resources and energy on interim priorities such as salvaging the last wild ferrets, improving ferret breeding capabilities, establishing a stable captive population, and enhancing the survival of reintroduced ferrets. Consequently, we are still struggling to determine what constitutes high quality ferret habitat, and what minimum prairie dog complex sizes (by prairie dog species) are needed to support viable ferret populations. Unfortunately, much of what we know is anecdotal and based on studies of small, fragmented ferret populations, or on the comparative success of specific reintroduction projects.

Given such uncertainties, it is impossible to provide definitive prairie dog habitat parameters for ferret recovery which could also serve as candidate conservation objectives for managing black-tailed prairie dogs. For that reason, I am uncomfortable with somewhat arbitrary prairie dog acreage targets for ferrets. At the recent BFFRIT Conservation Subcommittee meeting in

Denver last January, you suggested that states might develop or preserve 5,000 acre black-tailed prairie dog complexes as potential ferret recovery areas. Given the current status of black-tailed prairie dog populations and the paucity of large complexes over North America, development of one or two such complexes in each western state would be a significant achievement and would undoubtedly advance ferret recovery potential. However, given the comparative results of reintroduction efforts to date, 5,000 acre complexes would likely not support viable ferret populations and prairie dog complexes of 10,000+ acres may be needed (see additional discussion below). Furthermore, other factors such as colony distribution, topography, plague presence, etc. also influence overall site suitability.

Notwithstanding the above concern, ferret recovery is dependant on the restoration and conservation of large, stable prairie dog populations and proactive management of black-tailed prairie dog populations must move forward. We cannot forestall progress on prairie dog management by holding conservation plans to unspecified ferret habitat standards; yet, we also cannot establish fixed, arbitrary prairie dog habitat targets for ferrets that may ultimately prove unworkable. For conservation and recovery efforts to succeed, "adaptive management" principles must be applied, and must be flexible enough to alter management direction when warranted.

To understand the basis of expressed concerns over ferret habitat suitability, it may be useful to review the history and success of ferret reintroduction efforts:

- Ferrets were first reintroduced into the Shirley Basin, Wyoming in 1991 and since that time have been reintroduced into six other sites in five other states.

- Ferrets have been reintroduced into four black-tailed prairie dog complexes, two white-tailed prairie dog complexes, and one complex of Gunnison's prairie dogs. Beginning in 1996, the Service has prioritized the allocation of captive reared ferrets for reintroduction to sites with the best overall habitat characteristics – typically, large contiguous black-tailed prairie dog colonies which are free of sylvatic plague. Although reduced to a fraction of their historical numbers, black-tailed prairie dogs (the prairie dog species with the largest historical distribution and found throughout many Great Plains states from Canada to Mexico) often occupy large, contiguous colonies with substantially greater densities than either white-tailed prairie dogs or Gunnison's prairie dogs (species with more western and southwestern distributions).

- The most significant example of ferret reintroduction success and establishment of a self-sustaining wild population is a reintroduction effort in Conata Basin (on the Buffalo Gap National Grasslands, South Dakota). A total of 155 ferret kits were reintroduced into Conata Basin between 1996 and 1999. The ferret population in Conata Basin has exhibited exponential growth and has produced more wild kits in the year 2000 alone (168) than the total number of captive kits released (155); has experienced the highest documented short and long term survival rates of any reintroduction site; and, has a reproductive rate comparable to that of the last known wild population in Meeteetse, Wyoming (3.2 - 3.4 kits/female). A minimum of 242 wild ferrets were found at the Conata Basin reintroduction area in fall of 2000. The number of ferrets known to exist in the last naturally occurring population in Meeteetse, Wyoming was 128 animals at its peak.

- The Conata Basin site has about 13,000 acres of high density (14-18 prairie dogs/acre), plague-free black-tailed prairie dogs within a "7 km complex area" (Biggins, et al. 1993. USFWS Biological Report 13). Some 9000 acres of the best habitat exists in two large colonies which are within a single "core" population area (1.5 km or less apart). Prairie dog shooting was initially authorized outside of core ferret release areas but has been closed over the entire Basin since 1998. That closure resulted in a rapid prairie dog population resurgence over shooting areas and the ferret population has expanded into adjoining habitats.

- Preliminary information from a new reintroduction effort on the Cheyenne River Sioux Reservation in South Dakota indicates that short term survival of released ferrets is similar to that achieved in Conata Basin. The 7 km complex area on the Cheyenne River Reservation is slightly over 10,000 acres in size and the core ferret reintroduction area is about 5,200 acres of high density (12-14 prairie dogs/acre), plague-free black-tailed prairie dog habitat. The Cheyenne River Reservation has been identified as one of the remaining priority ferret reintroduction areas by the BFFRIT and we are optimistic that population growth and reintroduction success will be comparable to that of Conata Basin.

- A total of 171 ferret kits have been reintroduced into the UL Bend National Wildlife Refuge in Montana between 1994 and 1999. UL Bend is the second most successful reintroduction site to date. Kits have been born in the wild every year following the first release. Black-tailed prairie dog density has remained relatively high; however, the available acreage is limited (about 3000 acres within the core reintroduction area). The resulting annual ferret population has remained static and small. Production and survival rates are lower than those found in Conata Basin and population growth potential is limited due to the fragmentation and isolation of the UL Bend prairie dog colonies. Enhancing adjoining Bureau of Land Management and private lands to support larger, more closely distributed core complexes is needed to improve area habitat conditions and overall ferret recovery potential. Sylvatic plague has affected prairie dog colonies close to UL Bend but has not been documented within core towns.

- Between 1994 and 1999, a total of 217 ferrets were released in Badlands National Park, South Dakota, an area immediately adjoining Conata Basin. Some colonies within the Park have high prairie dog densities. However, the two principal core prairie complexes in Badlands are small (less that 1,000 acres each) and population levels withing these complexes have fluctuated substantially. Although wild production has been documented each year since the reintroduction program began, it appears that core colony size is to small to support long term, viable ferret populations. However, ferret dispersal between the Conata Basin and Badlands has been documented and the Badlands colonies may continue to support ferrets as the Conata Basin population grows and expands.

- A total of 167 ferrets have been released on the Ft. Belknap Indian Reservation in Montana between 1997 and 2000. Although the relative density of black-tailed prairie dog towns found on the core complex (Snake Butte) appears high, the acreage within the core area is limited (the principal colonies are about 1600 acres in size; outlying towns add approximately 600 acres). Short and long term survival and wild kit production have been limited. Plague has impacted portions of the Ft. Belknap Reservation, but has not directly impacted the Snake Butte Complex.

- Ferrets have also been released in white-tailed and Gunnison's prairie dog complexes in the Shirley Basin, Wyoming, in northwest Colorado/northeast Utah, and northwest Arizona. Varying degrees of success have been achieved but none to date approach the success obtained in black-tailed prairie dog colonies in South Dakota and Montana. Fifteen ferrets have persisted in the Shirley Basin five years after the last release of captive ferrets. All three sites have documented plague within or near core reintroduction areas.

- Although large, plague-free, black-tailed prairie dog complexes are afforded higher ferret allocation priority, the ferret recovery program will continue to focus recovery efforts in representative white-tailed and Gunnison's prairie dog complexes. To meet recovery objectives for establishing dispersed populations within the ferret's historical range it will be necessary to recover ferret populations outside the range of the black-tailed prairie dog.

- From the early stages of the ferret recovery program, program partners have worked to identify and prioritize suitable ferret reintroduction sites. In 1988, some 30 potential ferret reintroduction areas were identified across the ranges of all three prairie dog species. However, a more recent habitat assessment by the BFFRIT (a group of 27 partners from state and federal agencies, conservation organizations and Indian Tribes) found that only nine priority sites remain, seven of which are in black-tailed prairie dog complexes. Only five of the seven sites support large, plague-free black-tailed prairie dog complexes and would currently qualify as high priority reintroduction areas.

- The ferret recovery program is at a critical crossroad. Program partners have demonstrated that relatively large numbers of ferrets can be produced in captivity and that the means are available to successfully reestablishment wild ferret populations. However, limited habitat availability across North America precludes achievement of recovery goals for "downlisting" the species. Consequently, the ongoing, interstate effort to restore and manage black-tailed prairie dog habitat is essential for ferret recovery (and for the conservation of other sensitive, associate species).

Put into simplest terms – the only true measure of ferret reintroduction success to date suggests that high density, plague-free, black-tailed prairie dog complexes in excess of 10,000 acres, with large core colonies, and which are not subject to artificial perturbations (e.g. shooting/poisoning) are needed to reestablish wild ferret populations. Conversely, ferret reintroductions into smaller, more isolated, prairie dog complexes, have not successfully established stable ferret populations, even in complexes with relatively high prairie dog densities.

Given the above summary of ferret recovery experience, knowledge, and habitat availability assessments, I would like to offer a few recommendations which should be considered in the development of black-tailed prairie dog management plans and which are vital to ferret recovery.

1. **To the extent possible, preserve the last remaining large complexes of prairie dogs in their original configuration and size.**

Few high priority ferret reintroduction areas (large complexes of black-tailed prairie dogs) remain in North America and should be maintained to the maximum extent possible. Within the United States, these sites are restricted to two Forest Service grasslands in South Dakota and Wyoming and two South Dakota Indian Reservations. The largest remaining black-tailed prairie dog complex in North America is found in northern Chihuahua, Mexico. States, agencies, Tribes and private landowners (usually a mix of land ownership patterns is involved) who make provisions to preserve such sites should be given some elevated recognition/weight in any assessments over how responsibilities for black-tailed prairie dog management will ultimately be divided.

One concern I have about setting fixed prairie dog acreage targets for ferrets is that such an approach may lead to the loss of current habitat values for the few large complexes that remain. For example, if we assume that 5,000 acre complexes are needed to support ferrets, some may rationalize that existing, larger complexes could be reduced in size accordingly. In reality, the larger the site, the greater the potential benefits for ferrets. In addition, it may prove difficult to replace large colonies once they are lost, or may take an inordinate amount of time to recover.

2. **Provisions must be made in black-tailed prairie dog management plans to include a substantial number of large prairie dog complexes to support self-sustaining black-footed ferret populations.**

Again, although I believe that a target of 5,000 acre complexes is a good start, even larger core complexes should be encouraged to the extent possible (and perhaps given even greater, value-added weight). Given what is known from reintroduction efforts to date, it appears that complexes of 10,000+ acres are more appropriate for ferret recovery.

3. **Black-tailed prairie dog complexes identified for ferret recovery should be managed in a manner that ensures rapid establishment and long term stability of reintroduced ferret populations.**

The size of a given prairie dog colony alone would not ensure that a viable ferret population can become established or maintained over time. The following factors should be considered and/or incorporated in the development of management plans for prairie dog complexes used to help support ferret recovery:

a. Initially, at least, greater priority should be given to setting aside/restoring prairie dog colonies that exist in plague-free areas.
b. Prairie dog densities should be maintained at the high levels (14+ prairie dogs/acre) and human-caused, competing uses of prairie dog resources minimized (i.e. prairie dog shooting/poisoning). Although no definite correlations are yet available, high prairie dog densities may reduce the amount of surface acreage needed to support ferret populations. However, existing reintroduction efforts in high density complexes less than 5,000 acres have achieved only limited success.
c. Priority should be given to those sites with gentle, open topography and dominated by prairie/steppe grassland vegetation communities.
d. Grazing should be used as a management tool to help accelerate prairie dog

population growth and maintain colony vigor.

e. Prairie dog colonies within complexes should be distributed to facilitate ferret population establishment (i.e. core colonies should be spatially close together -- < 1.5 km apart).

f. To the extent possible, ferret recovery sites should be well distributed over and between states to promote spatial separation and help avoid catastrophic losses of ferret colonies through disease or natural disasters.

4. **Sylvatic plague is the most significant threat to both black-footed ferret recovery and black-tailed prairie dog conservation. Partners involved in planning efforts for both prairie dogs and ferrets should continue to focus attention and resources on investigations of the ecology and management of plague.**

5. **Interstate black-tailed prairie dog planning should be closely coordinated with BFFRIT planning and management efforts.**

   In recognition of the importance of black-tailed prairie dog restoration and conservation to ferret recovery, the BFFRIT Conservation Subcommittee has recommended (during its January 2001 meeting) that the BFFRIT remain closely involved in ongoing black-tailed prairie dog planning efforts. It was suggested that the Black-tailed Prairie Dog Interstate Coordinator and Black-footed Ferret Recovery Coordinator attend respective planning meetings to keep apprized of developments and provide support that would help facilitate the efforts of both groups.

I appreciate the difficult job the Interstate Black-tailed Prairie Dog Working Group faces and the substantial progress you've made to date. Again, I encourage the Working Group to move forward and adopt an open and adaptive approach to both prairie dog and ferret management. The Service and BFFRIT will continue to work closely with you, the Interstate Working Group, and other interested parties, to enhance conservation of both black-tailed prairie dogs and black-footed ferrets.

If you have any additional questions or comments, please call me at 307-721-8805.

Sincerely,

// signed//

J. Michael Lockhart
Black-footed Ferret Recovery Coordinator

cc. BFFRIT, Executive Committee and Conservation Subcommittee mailing lists

Ranching and Prairie Dogs

(invited paper)

Dustin Long ***Turner Endangered Species Fund***

Joe Truett ***Turner Endangered Species Fund***

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) historically occupied grasslands throughout much of the Great Plains and the American Southwest from Canada to Mexico (Hall 1981: 412-415). During the last 100 years this species has declined to a small fraction of its historic range and abundance because of eradication programs, loss of habitat and sylvatic plague (*Yersinia pestis*) (Miller et al. 1994). As more attention is focused on the plight of prairie dogs and the potential for their restoration, it becomes important to assess the compatibility of prairie dogs with ranching, the land-use practice most often associated with them.

Prairie dogs and large ungulates (hoofed mammals), primarily bison (*Bison bison*), evolved together. In much of their historically shared range, prairie dogs and wild ungulates developed a mutually beneficial relationship (Truett et al. 2001). The characteristic continual clipping of vegetation by prairie dogs improved the palatability of most grazing-resistant grasses by keeping them in an early growth stage. The availability of nutritious grasses in turn attracted ungulates, which grazed on and near prairie-dog colonies. The combination of large numbers of ungulates grazing and the mechanical impact of their hooves upon the earth improved horizontal visibility for prairie dogs, keeping them secure from predators and encouraging colony growth.

Suitable Vegetation Types for Prairie-dog Habitation

The three vegetation types most extensively occupied by prairie dogs are mixed-grass prairie, short-grass prairie and desert grasslands. The mutually beneficial relationship between prairie dogs and ungulates is most obvious in mixed-grass prairie (Krueger 1986). Here grazing by ungulates during the growing season may be required for prairie-dog colony survival, by improving prairie dogs' ability to see predators. Without grazing (or with deferred grazing schedules) colonies can quickly shrink and disappear (Knowles 1982). As a result and of ultimate benefit to ranchers, prairie-dog colony growth is most easily controlled in this vegetation type (Snell and Hlavachick 1980, Uresk et al. 1982, Cincotta 1985).

The short-grass prairie is probably the ideal habitat for prairie-dog colonization and persistence (Winter et al. 2002). Dominant grass species of this vegetation type include blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*). In most short-grass prairie settings, grazing by ungulates is not required for prairie-dog survival and expansion because the dominant grasses are naturally short (Truett et al. 2001). As a consequence, controlling prairie-dog colony growth in this vegetation type may be difficult by managing grazing regimes alone.

In general, the least productive and least studied of the three vegetation types are the desert grasslands. Historically fewer bison and prairie dogs were found in this vegetation type than in mixed-grass and short-grass prairies. Rainfall is more sporadic than in the Great Plains, and some of the dominant grasses in this vegetation type are less resilient to continuous grazing pressure. As a result, sustainable ungulate stocking rates and prairie- dog densities are commonly lower in the desert grasslands than in the other grassland types. Grazing by ungulates may be required during plant growth periods for prairie-dog survival, however this grassland type can be susceptible to rapid degradation under the combined grazing pressure of both prairie dogs and ungulates.

Vegetative Response to Grazing

Regardless of vegetation type, the combined grazing of ungulates and prairie dogs causes shifts in plant species composition. Most obvious are the increases in grazing-tolerant plant species and the decline or disappearance of grazing-intolerant species. Intensive grazing by prairie dogs tends to replace grasses with forbs (broad-leafed herbaceous cover). Heavy grazing by prairie dogs and ungulates also will cause a shift from tall and mid-height grasses to those of shorter stature (Detling 1998, Truett et al. 2001).

Some productive sites (see below) may show an increase in net annual primary production when exposed to the combined grazing of prairie dogs (Williamson et al. 1989) and ungulates, which enhances soil fertility and stimulates plant growth (O'Meilia et al. 1982, Detling 1998). But in most cases moderate grazing is generally recommended because it keeps the vegetation in an early growth state and provides more nutritional value and less standing dead material for grazers (Detling 1998). One problem of course is that prairie dog grazing intensity is difficult to manage, and in dry years prairie dogs may consume most of the annual growth within colonies, leaving little for livestock.

Site Productivity

Another consideration when addressing the compatibility of large grazers and prairie dogs is site productivity, a good measure of which is precipitation, or more accurately, available soil moisture. The better-watered sites tend to support taller grasses and produce more forage for grazers. Productivity can vary dramatically from year to year depending on rainfall, especially in the desert grasslands. Regardless of vegetation type, productive sites usually will require more intense grazing by ungulates than less productive sites in order to keep the grass short and thereby optimum for prairie dogs.

Prairie Dogs and Ungulate Stocking Rates

Stocking levels of cattle or other ungulates play an important role in managing prairie dogs. In most cases, heavy overgrazing, especially in the growing season, will increase prairie dog colony acreage but reduce prairie dog densities. Summer-deferred grazing schedules in more productive grasslands may lead to a decrease in colony acreage but an increase in prairie dog densities.

Stocking rates can be used as a tool to help manage prairie-dog densities and colony growth on productive sites (Uresk et al. 1982, Cincotta 1985). On such sites grazing duration and intensity determine in large part the ability of prairie-dog colonies to persist and expand. The historical abundance of prairie dogs in higher-rainfall parts of the Great Plains regions apparently was tied to high stocking rates of bison or cattle (Truett et al. 2001).

Prairie-dog Colony Age

As prairie-dog colonies age, the center of the colony tends to shift from grasses to forbs and annuals (Detling 1998). Most ungulates, except for forb-feeders such as pronghorn antelope (*Antilocapra Americana*), tend to reject these areas in preference for newly colonized areas (perimeter of prairie dog colony) where grasses are more abundant. Thus a young prairie dog colony often becomes less beneficial to cattle as it ages.

Conclusion

We have found that prairie-dog restoration and ranching can be compatible and in many cases mutually beneficial. The degree of compatibility between prairie dogs and ranching largely depends on vegetation type and production, ungulate stocking rates, acreage occupied by prairie dogs, and colony age. To manage both prairie dogs and ungulates effectively does require some measure of flexibility and knowledge. Based on our experience and that of others, ranching and prairie dogs can best coexist when smaller, younger prairie-dog colonies are scattered over the landscape and occupy approximately 20 percent or less of the available habitat. Ranching can continue with or without prairie dogs, but prairie dogs may need ranching throughout a significant portion of their range in order to persist.

Literature Cited

Cincotta, R.P. 1985. Habitat and dispersal of black-tailed prairie dogs in Badlands National Park. Ph.D. Dissertation. Fort Collins, CO.: Colorado State University.

Detling, J.K. 1998. Mammalian herbivores: ecosystem-level effects in two grassland national parks. Wildlife Society Bulletin. 26:438-448.

Hall, E.R. 1981. The Mammals of North America. Vol 1. 2nd ed. New York: John Wiley and Sons, Inc. 600 p.

Knowles, C.J. 1982. Habitat affinity, populations, and control of black-tailed prairie dogs on the Charles M. Russell National Wildlife Refuge. Ph.D. thesis, University of Montana. 171 p.

Krueger, K. 1986. Feeding relationships among bison, pronghorn and prairie dogs: an
experimental analysis. Ecology. 67:760-770.

Miller, B.; Ceballos, G.; Reading, R. 1994. The prairie dog and biotic diversity. Conservation Biology. 8:677-681.

O'Meilia, M.E.; Knopf, F.L.; Lewis, J.C. 1982. Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management. 35:580-585.

Snell, G.P.; Hlavachick, B.D. 1980. Control of prairie dogs—the easy way. Rangelands. 2:239-240.

Truett, J.C.; Phillips, M.; Kunkel, K.; Miller, R. 2001. Managing bison to restore biodiversity. Great Plains Research. 11:123-144.

Uresk, D.W.; MacCracken, J.G.; Bjugstad, A.J. 1982. Prairie dog density and cattle grazing relationships. P. 199-201. In, R.M Timm and R. J. Johnson, eds. Fifth Great Plains Wildlife Damage Control Workshop Proceedings. October 13-15, 1981. Lincoln, NE: University of Nebraska.

Williamson, S.C.; Detling, J.K.;Dodd, J.L.; Dyer, M.I. 1989. Experimental evaluation of the grazing optimization hypothesis. Journal of Range Management. 42:149-152.

Winter, S.L.; Cully, J.F.; Pontius, J.S. 2002. Vegetation of prairie dog colonies and non-colonized short-grass prairie. Journal of Range Management. 55:502-508.

La Actividad Ganadera y los Perros Llaneros

(resumen)

Dustin Long *Turner Endangered Species Fund*
Joe Truett *Turner Endangered Species Fund*

Los perros llaneros de cola negra (*Cynomys ludovicianus*) han ocupado históricamente pastizales a través de gran parte de las Grandes Praderas y del suroeste americano, desde Canadá hasta México (Hall 1981: 412-415). Durante los últimos 100 años, la especie ha disminuido a una pequeña fracción de su rango y abundancia histórica a causa de programas de erradicación, pérdida de hábitat y a la plaga silvática, *Yersinia pestis* (Miller et al. 1994). A medida que nos enfocamos en la situación del perro de la pradera y del potencial para restauración, es evidente la importancia de evaluar la compatibilidad de los perros llaneros con la actividad ganadera.

Los perros llaneros y los mamíferos grandes, principalmente el bisonte (*Bison bison*), evolucionaron juntos. En gran parte de su historia compartida, los perros llaneros y los mamíferos salvajes desarrollaron una relación mutuamente benéfica, que mejoraba la calidad del forraje y que también mejoraba la visibilidad horizontal del terreno para los perros llaneros (Truett et al. 2001).

Tipos de Vegetación Apropiados Para Sobrevivencia del Perro Llanero

Los tres tipos de vegetación más asociados con los perros llaneros son la pradera mezclada, la pradera de pequeñas gramíneas y los pastizales desérticos. La relación mutuamente benéfica entre el perro de la pradera y el ganado rumiante es más obvia en la pradera mezclada (Krueger 1986).

La pradera baja es quizá el hábitat ideal para la colonización y persistencia del perro de la pradera (Winter et al. 2002). En la mayoría de estos entornos, no se requiere que los rumiantes pasten en la zona para que sobrevivan los perros llaneros, porque el pasto dominante es naturalmente bajo (Truett et al. 2001). En consecuencia, el controlar el crecimiento de las colonias de perros llaneros en este tipo de vegetación puede ser difícil si se manejan regimenes de pastoreo en forma aislada.

En general, los pastizales desérticos son el tipo menos productivo y menos estudiado de los tres tipos de vegetación. Históricamente, hay menos bisonte y perro de la pradera en estas áreas. La precipitación es más esporádica que en las Grandes Praderas, y algunos de los pastos dominantes en este tipo de vegetación son menos resistentes al pastoreo continuo. Como consecuencia, las capacidades de carga para sostener ungulados y poblaciones de perros llaneros son mas bajas en los pastizales de desierto que en otros tipos de pastizal. El pastoreo por ungulados puede ser requerido durante los períodos de crecimiento vegetal para asegurar la sobrevivencia de los perros llaneros, sin embargo este tipo de pastizal puede ser susceptible de una rápida degradación bajo una presión de pastoreo combinada por ungulados y perros llaneros.

Respuesta de la Vegetación Al Pastoreo

Sin importar el tipo de vegetación, el pastoreo combinado de rumiantes y perros llaneros ocasiona cambios en la composición de las especies de plantas. Lo más obvio es el aumento de especies de plantas más tolerantes, y la disminución o desaparición de las menos tolerantes. Un pastoreo intensivo por perros llaneros tiende a reemplazar gramíneas por hierbas. Un pastoreo pesado por perros llaneros y rumiantes ocasiona también un cambio gramíneas altas y medianas a zacates de baja estatura (Detling 1998, Truett et al. 2001).

Algunos sitios productivos pueden mostrar un incremento en producción primaria neta cuando son expuestos a un pastoreo combinado con perros llaneros y ungulados (Williamson et al. 1989), lo cual mejora la fertilidad del suelo y estimula el crecimiento vegetal (O'Meilia et al. 1982, Detling 1998). Pero en la mayoría de los casos se recomienda un pastoreo moderado, porque mantiene la vegetación en una etapa de crecimiento temprana, y se proporciona más valor nutritivo y menos material vegetal muerto para el ganado (Detling 1998).

Productividad del Sitio

Otra consideración, al tocar el tema de la compatibilidad entre ganado grande y perros llaneros, es la productividad del sitio. Una buena medida de la productividad es la precipitación. Los sitios con más agua tenderán a sustentar pasto más alto y producirán más forraje. La productividad puede variar dramáticamente año con año, dependiendo de la precipitación, especialmente en los pastizales desérticos.

Tasas de Carga Animal Para Perros Llaneros y Rumiantes

La densidad de ganado juega un papel importante en el manejo de las densidades de los perros llaneros y el crecimiento de sus colonias. En la mayoría de los casos el pastoreo pesado aumentará el área de la colonia de perros llaneros, pero reducirá su densidad. De la misma forma, el pastoreo en pastizales más productivos puede llevar a una disminución en el área de la colonia, pero a un aumento en sus densidades.

Las tasas de carga pueden ser usadas como una herramienta para manejar densidades de perros de las praderas y crecimiento de las colonias en sitios productivos (Uresk et al. 1982, Cincotta 1985). En tales sitios, la intensidad y duración del pastoreo determina en gran parte la habilidad de las colonias de perros llaneros para persistir y expandirse. La abundancia histórica de los perros llaneros en lugares de alta precipitación de las regiones de las Grandes Praderas, aparentemente fue sujeta a tasas elevadas de carga animal por bisonte o ganado doméstico (Truett et al. 2001).

Edad de las Colonias de Perros Llaneros

A medida que las colonias de perros llaneros envejecen, los patrones de vegetación tienden a cambiar. El ganado tiende a rechazar estas áreas, prefiriendo áreas recientemente colonizadas, donde el pasto es más abundante.

Conclusión

Hemos encontrado que la restauración de las colonias de perros llaneros y las actividades ganaderas pueden ser compatibles y en muchos casos, mutuamente benéficas. El grado de compatibilidad entre los perros llaneros y las actividades ganaderas depende en gran medida del tipo de vegetación y la producción, la densidad de ganado, el área ocupada por las colonias de perros llaneros y la edad de la colonia. Los perros llaneros y las actividades ganaderas pueden coexistir mejor cuando las colonias son jóvenes, más pequeñas, están distribuidas en la zona, y ocupan un 20% o menos del hábitat disponible.

Literatura Citada

Cincotta, R.P. 1985. Habitat and dispersal of black-tailed prairie dogs in Badlands National Park. Ph.D. Dissertation. Fort Collins, CO.: Colorado State University.

Detling, J.K. 1998. Mammalian herbivores: ecosystem-level effects in two grassland national parks. Wildlife Society Bulletin. 26:438-448.

Hall, E.R. 1981. The Mammals of North America. Vol 1. 2nd ed. New York: John Wiley and Sons, Inc. 600 p.

Knowles, C.J. 1982. Habitat affinity, populations, and control of black-tailed prairie dogs on the Charles M. Russell National Wildlife Refuge. Ph.D. thesis, University of Montana. 171 p.

Krueger, K. 1986. Feeding relationships among bison, pronghorn and prairie dogs: an experimental analysis. Ecology. 67:760-770.

Miller, B.; Ceballos, G.; Reading, R. 1994. The prairie dog and biotic diversity. Conservation Biology. 8:677-681.

O'Meilia, M.E.; Knopf, F.L.; Lewis, J.C. 1982. Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management. 35:580-585.

Snell, G.P.; Hlavachick, B.D. 1980. Control of prairie dogs—the easy way. Rangelands. 2:239-240.

Truett, J.C.; Phillips, M.; Kunkel, K.; Miller, R. 2001. Managing bison to restore biodiversity. Great Plains Research. 11:123-144.

Uresk, D.W.; MacCracken, J.G.; Bjugstad, A.J. 1982. Prairie dog density and cattle grazing relationships. P. 199-201. In, R.M Timm and R. J. Johnson, eds. Fifth Great Plains Wildlife Damage Control Workshop Proceedings. October 13-15, 1981. Lincoln, NE: University of Nebraska.

Williamson, S.C.; Detling, J.K.;Dodd, J.L.; Dyer, M.I. 1989. Experimental evaluation of the grazing optimization hypothesis. Journal of Range Management. 42:149-152.

Winter, S.L.; Cully, J.F.; Pontius, J.S. 2002. Vegetation of prairie dog colonies and non-colonized short-grass prairie. Journal of Range Management. 55:502-508.

Potential black-footed ferret reintroduction sites, 2008.

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ABSTRACT

In 2003, I developed a new, broad list of active and potential black-footed ferret reintroduction sites across the historic range (Luce 2005a). I listed 9 active reintroduction sites, 3 immediate potential sites which might support black-footed ferrets in <3 years, and 70 new sites that might meet the biological and habitat suitability requirements for reintroduction of the black-footed ferret within 3-10 years (intermediate potential). I now expand this conceptual effort using prairie dog survey data generated since 2003 to list 18 active, 3 immediate potential, and 181 intermediate potential sites in 12 states, 1 Canadian province, and 1 Mexican state. Intermediate potential sites include: Arizona: 10; Colorado: 27; Kansas: 19; Montana: 9: Nebraska: 25; New Mexico: 7; North Dakota: 7; Oklahoma: 5; South Dakota: 13; Texas: 21, Utah: 12, and Wyoming: 26. The best available data were used for each state; however the precision level of the survey data varied between states. Some Colorado and Texas counties contain several complexes. Colorado complexes are identified separately, Texas complexes are not. Nebraska has not compiled data on location of complexes therefore I list all counties which contain >607.5 ha of colonies. I list 58 intermediate potential sites in Nebraska, North Dakota, Oklahoma, and Texas; states which currently do not have any active black-footed ferret reintroduction sites.

I contacted local experts and reviewed the published and unpublished literature describing colony locations for three species of prairie dogs, evaluating only the biological potential of prairie dog complexes to support black-footed ferrets based on current or past survey data. I did not discount sites currently impacted by plague since viable plague management options may become available within 10 years. This paper does not constitute a proposed state or federal action at any of the proposed sites; it is merely a conceptual approach to aid in black-footed ferret recovery by identifying potential reintroduction sites at a gross level. Actual development of a reintroduction site will be contingent upon directed management emphasis, state and federal agency management priority, and, if on private land, landowner concurrence through agreements or incentives. Four sites I listed as having intermediate potential in 2003 (Luce 2005a) were elevated to active reintroduction sites between 2003 and 2008. An additional site on a private ranch in Arizona also became an active site, making a total of 5 new sites in 5 years.

Key words: prairie dog, black-footed ferret, reintroduction, *Cynomys*, *Mustela nigripes*, conservation, endangered species

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INTRODUCTION

The latest published version of the Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service 1988) listed several downlisting criteria, one of which is to establish reintroduced black-footed ferret populations across the species' historical range proportional to the distribution and abundance of historical habitats. Since the states of Nebraska, North Dakota, Oklahoma, and Texas do not currently have active reintroduction sites, identification of 58 ntermediate potential sites in those states is especially important to aid in meeting Recovery Plan distribution objectives.

The new Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service in prep. 2008) will undoubtedly contain a reintroduction site selection process, downlisting, and delisting goals. The current downlisting goal (U.S. Fish and Wildlife Service 1988) of 1500 breeding adults in 10 or more populations, with no fewer than 30 breeding adults in any population, will likely carry over into the new plan. Assuming an average black-tailed prairie dog density, this goal would require a minimum of 75,000 ha of black-tailed prairie dog colonies. But since some of the black-footed ferret populations will be in white-tailed or Gunnison's prairie dog colonies, which occur at lower densities, the total prairie dog occupied area needed to meet the Black-footed Ferret Recovery Plan objective will certainly exceed 75,000 ha.

Given experiences with black-footed ferret management at Meeteetse, Wyoming from 1981 until disease forced removal of the last black-footed ferret in 1987 (Biggins 2003); large prairie dog die-offs due to plague in Phillips County, Montana between 2000 and 2007 (Matchett pers comm. 2008); and the 2008 outbreak of plague in previously plague-free Conata Basin, South Dakota (Larson pers comm. 2008) it is evident that a large number of reintroduction sites must be concurrently active, and several more fully ready to receive black-footed ferrets if unexpected, rapid loss of habitat at a given site requires sudden translocation of black-footed ferrets. In addition to sites maintained at ready, many additional widely separated sites must be in various stages of development in the 3-10 year timeframe. I offer a new baseline list that includes contributions from all portions of the species' historic range, including 181 sites identified from pre- and post-2003 survey data.

As with my previous attempt to develop a list of potential reintroduction sites, this effort is not constrained by the need to immediately take into account land ownership, prevalent landowner attitudes in the area, plague history, weather history, or other factors that will eventually affect on-the-ground site planning efforts. It is merely an attempt to highlight areas where reintroduction could occur based on the following minimum criteria: 1) the site must be currently occupied by prairie dogs, and 2) the site must either contain enough prairie dogs to support a viable black-footed ferret population now, or have sufficient potential habitat to expand to support a black-footed ferret population within 3-10 years.

There are issues other than the two listed above that must be addressed when actually developing reintroduction sites, however, recovery of the black-footed ferret depends heavily upon identifying and conserving areas that meet or have the potential to meet the biological parameters for long-term survival of viable populations. Social and economic issues, including private lands rights, economic concerns related to forage competition between livestock and prairie dogs, and others, are vitally important. Political and social barriers often surpass biological issues in difficulty. But, given sufficient time and goodwill, many such obstacles can be equitably overcome. Changes in federal land management priorities, cooperative management planning on federal lands, and financial incentives or regulatory assurances for private landowners or tribal governments must logically follow site identification if development is to become a reality. The critical need is to identify suitable sites and begin management of those sites for reintroduction and recovery.

One example illustrates how significant plague, weather factors, and habitat changes affect site suitability over time. In 1988-89, using primarily BLM and Wyoming Game and Fish Department unpublished data, I listed 18 potential black-footed ferret reintroduction sites in Wyoming; sites where over 2,025 ha of active white-tailed prairie dog colonies had been mapped in the 1980’s. Conway (1989) evaluated 6 of those sites and concluded that only two had prairie dog numbers suitable for black-footed ferret reintroduction in 1989. Many of those sites in Wyoming are still not suitable nearly 20 years later, primarily due to periodic population suppression by plague (Grenier pers comm. 2008). A similar situation undoubtedly exists throughout the range of the black-footed ferret.

An area where plague has never been documented is probably preferable for black-footed ferret reintroduction. But new data indicating maintenance of both prairie dog and black-footed ferret populations on a landscape scale in Shirley Basin, Wyoming where plague epizootics occur sporadically indicates that a totally plague free area is not necessary (Grenier 2008). In addition, translocation of black-footed ferrets from sites which develop plague to sites that are plague-free at the time of need must be considered as a black-footed ferret management option.

Black-footed ferrets have been released at new sites at a rate of one site per year over the last 5 years. In addition, several states have developed or refined prairie dog mapping data making it possible to identify new potential sites or split existing sites into 2 or more potential sites. Land ownership, and political and social attitudes constantly change, resulting in new opportunities for management.

Identifying a large number of sites will make it such that no one site will be under pressure for rapid development. However, the presence of a site on the list will allow agencies to begin planning towards management of the site for black-footed ferret reintroduction in 3-10 years.

METHODS

Sites identified previously (Luce 2005a) are listed if still relevant, usually with updated information. I also list new sites or sub-sites identified from post-2003 publications or 2008 personal communications. I used information from 10 state prairie dog management plans, white-tailed prairie data from Seglund et al. (2004) and Gunnison's prairie dog data from Western Association of Fish and Wildlife Agencies (2007).

New information was acquired for 7 Native American Reservations, 1 state in Mexico, 1 Canadian province, and all states within the historic range of the black-footed ferret except Oklahoma.

I use the following terminology: 1) Active Sites are those at which black-footed ferrets have been released and are being actively managed, 2) Immediate Potential Sites at which planning is underway and reintroduction is expected to occur within 1-3 years, and 3) Intermediate Potential Sites at which opportunities may exist in the 3-10 year time frame.

Planning efforts conduced by recovery partners require a queue of potential sites. I provide a locally specific list of all potential black-footed ferret reintroduction sites across the species' historic range, but focus on Intermediate Potential Sites since these provide the next step in black-footed ferret reintroduction beyond management of Active and Immediate Potential Sites. Although I surmise that Long-term Potential Sites may exist, I do not list those in this paper.

A complex is defined as contiguous habitat in which no colony is farther than 7 km from another colony (Biggins et al. 1993). This definition was applied at existing black-footed ferret reintroduction sites and in most state prairie dog management plans. A colony is defined as a concentration of black-tailed prairie dogs with an average density of at least 4.05 individuals per ha (Luce 2003), or a concentration of white-tailed or Gunnison's prairie dogs with a minimum of 20 burrow openings per ha on 5-ha parcels (Biggins et al. 1993; Seglund et al. 2004; Western Association of Fish and Wildlife Agencies 2007). Although density data were not used when identifying Intermediate Potential Sites in this paper it must be assumed that sites would be required to meet minimum density requirements before black-footed ferret reintroduction would take place.

Based on Biggins et al. (1993) and known densities of the respective species, I began with the premise that the minimum adult population of 30 black-footed ferrets identified in the 1988 Recovery Plan (U.S. Fish and Wildlife Service 1988) might require 1,215 ha of contiguous black-tailed occupied prairie dog habitat, 1823 ha of contiguous occupied Gunnison's prairie dog habitat, or 2,430 ha of contiguous occupied white-tailed prairie dog habitat. I recognize that prairie dog densities vary between sites and at individual sites on an annual basis, but I found it necessary to use averages in this evaluation process.

I also work from the premise that the amount of extant, occupied habitat noted above may not be necessary to identify potential reintroduction sites and perhaps begin black-footed ferret releases. I suggest that 607.5 ha of contiguous occupied black-tailed prairie dog habitat, 911.3 ha of contiguous occupied Gunnison's prairie dog habitat, or 1,215 ha of contiguous occupied white-tailed prairie dog habitat may be sufficient to begin management planning or possible experimental release of black-footed ferrets. The choice of 50% was arbitrary and assumes that prairie dog colonies can grow rapidly as has been demonstrated at black-tailed prairie dog complexes in New Mexico (Long pers comm. 2008), Colorado (Hastings pers comm. 2008), Kansas (Manes pers comm. 2008), Arizona (Van Pelt pers comm. 2008), and North Dakota (Knowles 2007). Of course, many other factors may affect suitability considerations at a reintroduction site, but I believe these rough measures may allow preliminary identification of a queue of sites that can be further evaluated.

I characterized sites by species of prairie dog present, the amount of occupied prairie dog habitat, disease status, etc, in a manner similar to Lockhart (1998-2007). Most of these sites have been identified as a result of recent inventories of prairie dog habitat by state, tribal, university, or other entities.

RESULTS

Current and potential black-footed ferret reintroduction sites are listed for the historic range of the species (Tables 1 and 2) (Figure 1). General background information related to the prairie dog population in the state or province is presented first, followed by site descriptions. Many sites are in the early stages of identification and mapping, particularly those identified from aerial surveys and/or those occurring on private land. The best available data were used for each state, however, the precision level of the survey data varied between states. A best estimate of plague status was made in Tables 1 and 2 based on either site specific data provided by the respective state or the location of the site in respect to the plague line (Cully et al. 2006). Due to the great number of unknowns related to plague, the status may change quickly at a given site.

ARIZONA

Black-tailed and Gunnison’s prairie dogs occurred in Arizona historically. The black-tailed prairie dog was extirpated from southern Arizona in the 1930’s and although reintroduction will begin on Las Cienegas National Conservation Area near Sonoita in 2008, expansion to 607.5 ha within 10 years is unlikely (Van Pelt pers comm. 2008), therefore the site is not listed in this publication. Gunnison’s prairie dogs are located in northern Arizona from the Colorado River to Flagstaff and eastward along the Little Colorado River. As much as 1/3 of the known range occurs on the Navaho Reservation.

Active Sites

Aubrey Valley: Black-footed ferret reintroduction efforts began in 1996 in a Gunnison’s prairie dog complex spread over parts of Coconino, Yavapai, and Mojave Counties in the northwestern part of the State (Fig. 1). Releases of captive black-footed ferrets are ongoing. Approximately 60 black-footed ferrets occur in the wild at present (Van Pelt pers comm. 2008). Total occupied habitat is approximately 12,039 ha with a mixture of private, state, and Hualapai Reservation lands. Monitoring at this site has not documented plague during the last 20 years, although it has been noted in the region. Prairie dog populations can be severely affected by drought at this site

(Lockhart 1998-2007)

Espee Ranch: This Gunnison's prairie dog complex is on the Coconino Plateau northwest of Aubrey Valley and west of Cataract Canyon. Prairie dog currently occupy 11,745 ha, a considerable increase from an estimated 1,215 ha mapped in the 1980's. The site includes 2 large colonies and a number of smaller colonies. Plague has been documented but not recently. Forty-four black-footed ferrets were released on-site in 2007 and additional releases are planned in 2008 (Van Pelt pers comm. 2008).

Intermediate Potential Sites

Canyon Diablo: The Gunnison's prairie dog complex located near Canyon Diablo between Winslow and Flagstaff contained 12 colonies in 1994 (Arizona Game and Fish Department and Navaho Natural Heritage Program 1996). Very few people live within the complex. Mapping planned for 2008 will provide updated information (Mikesic pers comm. 2008).

Coconino Plateau (East of Cataract Canyon): This Gunnison's prairie dog complex is on the Coconino Plateau northwest of Aubrey Valley and east of Cataract Canyon. The colonies have not been mapped recently but mapping is scheduled in 2008 (Van Pelt pers comm. 2008). Prairie dog acreage on Espee Ranch west of Cataract Canyon increased acreage dramatically between the 1980's and the present. If colonies east of the canyon responded similarly, a large complex capable of supporting black-footed ferrets may exist.

Coconino Plateau (Navaho Nation): Gunnison's prairie dogs occur on Navaho lands on the Coconino Plateau northwest of Aubrey Valley and west of Cataract Canyon in the vicinity of Espee Ranch (Wagner et al. 2006). Additional mapping will take place in 2008 (Mikesic pers comm. 2008). Since black-footed ferrets were successfully released on Espee Ranch in 2007 and additional releases are planned in 2008, this complex could potentially support black-footed ferrets within 10 years.

East of Flagstaff: A complex west of the Little Colorado River, east of Flagstaff, has been impacted by plague but some colonies were still active in 2001 (Wagner et al. 2006), therefore the complex could recover and support black-footed ferrets within 10 years.

East of Seligman: Approximately 2,502 ha of active Gunnison's prairie dogs colonies were present on-site in 1992. The site is a large, open grassland bisected by the I-40. Occupied habitat was reduced considerably in 1996 due to a plague epizootic. This area is <10 km from Aubrey Valley (Wagner and Drickamer 2002; Wagner pers comm. 2008).

Elephant Butte: The Gunnison's prairie dog complex located west of Dilkon contained 70 colonies in 1994 (Arizona Game and Fish Department and Navaho Natural Heritage Program 1996). Mapping planned for 2008 will provide updated information (Mikesic pers comm. 2008). This may be part of or separate from the general area described (see below) as West of Dilkon.

Leupp: The Gunnison's prairie dog complex located near Luepp northwest of Winslow contained 5 colonies in 1994 (Arizona Game and Fish Department and Navaho Natural Heritage Program 1996). There are houses, highways, etc. within the complex. Mapping planned for 2008 will provide updated information (Mikesic pers comm. 2008).

Red Lake: The Gunnison's prairie dog complex located northwest of Luepp contained 3 colonies in 1994 (Arizona Game and Fish Department and Navaho Natural Heritage Program 1996). Mapping planned for 2008 will provide updated information (Mikesic pers comm. 2008).

West of Dilkon, Navajo Nation: The Navajo Natural Heritage Program surveyed Gunnison's prairie dogs in this area to investigate its potential as a black-footed ferret reintroduction site. The survey documented approximately 3,200 ha of occupied habitat. This area was affected by plague in 1996, and there has been little recovery to date (Wagner and Drickamer 2002; Wagner pers comm. 2008).

West of Wupatki National Monument: North of Flagstaff. Gunnison's prairie dogs are present at this site. A complex of 950 ha was mapped in 2001. Plague has occurred but the extent has not been quantified (Wagner and Drickamer 2002; Wagner pers comm. 2008).

COLORADO

Black-tailed prairie dogs, white-tailed prairie dogs, and Gunnison's prairie dogs occur in Colorado. Black-tailed prairie dogs occur in all counties in the historical range in the eastern one-third of the state, and recent surveys indicate 255,596 ha of occupied habitat (Colorado Division of Wildlife 2003a). At the time of data assimilation for Luce (2005a) these data were not available therefore older data (EDAW Inc. 2000) were used to identify the 10 counties with the largest amount of active, occupied habitat in the state. Colorado Division of Wildlife (2003a) presents a more accurate representation of black-tailed prairie dog distribution over the eastern plains and identifies 18 complexes which have the biological potential to support black-footed ferrets. Some counties in Colorado contain several complexes (see below).

Active Sites

Wolf Creek: White-tailed prairie dogs occupy this site in northwestern Colorado in Moffat and Rio Blanco Counties along the Utah (Uintah County) and Wyoming (Sweetwater County) borders, and the complex extends into both Utah and Wyoming. Reintroduction began in 2001. A total of 209 black-footed ferrets have been released to date and releases are ongoing. At least 13 black-footed ferrets occur in the wild at present. Total occupied prairie dog habitat is approximately 20,250 ha, primarily on U.S. Bureau of Land Management (BLM) land. Plague is present. Potential habitat present in the Colorado portion of this site is estimated at 45,553 ha (Lockhart 1998-2007).

Immediate Potential Sites

Fort Carson: The black-footed ferret recovery program is actively working to bring black-footed ferrets to this site in the near future. Black-tailed prairie dogs occupy 80 colonies at the site which is on a U.S. Army installation. Approximately 1,418 ha of occupied habitat were present before a plague outbreak occurred in 2002, but the occupied area had increased to 2,609 ha in 2007. One colony of 960 ha exists, and 5.5 Km away is a complex of 4 colonies totaling 570 ha (Rick Clawges pers comm. 2008). The site is protected from shooting and poisoning except where black-tailed prairie dogs may constitute a human health hazard (Woodson pers comm. 2003). A large area of occupied habitat also occurs on private lands adjacent to Ft. Carson, particularly along the southern boundary in Pueblo County and may approach 2,000 ha (EDAW Inc. 2000; Colorado Division of Wildlife 2003a; Rick Clawges pers comm. 2008).

Intermediate Potential Sites

Black-tailed Prairie Dogs

Complexes identified below were identified during aerial surveys conducted by the Colorado Division of Wildlife in 2002. Complex is defined as a group of colonies totaling more than 2,025 ha and with a density >10 colonies/150 Km^2 (Colorado Division of Wildlife 2003a).

Baca County: Black-tailed prairie dog colonies occupy 29,155 ha, occur over most of the county, and inhabit 4.39 percent of the land area. Two complexes are known to exist. Complex #17, approximately 15 miles northeast of Springfield, contained 4 large colonies; and Complex #18, approximately 20 miles west of Springfield contained 17 colonies. This county is primarily private land.

Bent County: Black-tailed prairie dog colonies occupy 32,588 ha, occur over most of the county, and inhabit 8.30 percent of the land area. Three complexes are known to exist. Complex #11, which covers much of the northern one-quarter of the county, north of Highway 50, contained 86 colonies; Complex #14, approximately 15 miles southeast of Las Animas contained 9 colonies; and Complex #15, approximately 18 miles southwest of Lamar contained 5 large colonies. This county is primarily private land.

Crowley County: Black-tailed prairie dog colonies occupy 9,087 ha, occur over most of the county, and inhabit 4.38 percent of the land area. Only one complex is known to exist, and is mostly in adjacent Pueblo County. This county is primarily private land.

Kit Carson County: Black-tailed prairie dog colonies occupy 7,333 ha, occur mostly in the eastern one-half of the county, and inhabit 1.31 percent of the land area. One complex is known to exist. Complex #8, approximately 15 miles north of Burlington, contained 38 colonies. This county is primarily private land.

Prowers County: Black-tailed prairie dog colonies occupy 27,129 ha, occur over most of the county, and inhabit 6.36 percent of the land area. Three complexes are known to exist. Complex #12, approximately 14 miles northeast of Lamar, contained 22 large colonies; Complex #13, approximately 25 miles northeast of Lamar, contained 61 colonies; and Complex #16, approximately 25 miles north of Springfield, contained 39 colonies. This county is primarily private land.

Pueblo County: Black-tailed prairie dog colonies occupy 18,420 ha, occur mostly in the northern and eastern parts of the county, and inhabit 2.96 percent of the land area. Two complexes are known to exist. Complex #9, approximately 10 miles north of Pueblo, contained 24 colonies; and Complex #10, approximately 30 miles northeast of Pueblo contained 14 colonies. This county is primarily private land.

Weld County: Black-tailed prairie dog colonies occupy 21,318 ha, occur mostly in the southern two-thirds of the county, and inhabit 2.05 percent of the land area. Five complexes are known to exist. Complex #1, approximately 25 miles west of Sterling, contained 17colonies; Complex #2, approximately 30 miles northeast of Greeley, contained 16 colonies; Complex #3, approximately 20 miles northeast of Greeley, contained 9 colonies; Complex #4, stretching between Greeley and Ft. Collins, contained 89 colonies, many of which may occur in an urban setting unsuitable for black-footed ferret occupancy; and Complex #5, including Denver, Ft. Collins, their suburbs, and several small towns, contained 127 colonies, most of which may occur in an urban setting unsuitable for black-footed ferret occupancy. Complexes #4 and #5 are included in this analysis because the eastern parts of the counties are still rural and therefore some part of the complex could function as a black-footed ferret reintroduction site in at least the short term. This county is a mixture of public and private land.

Other Sites

Cimarron National Grassland: Black-tailed prairie dogs occupy this site, which has approximately 16,200 ha of potential habitat. According to the Cimarron National Grassland, prairie dogs occupied 1,296 ha in 2003, and 2,292 ha in 2006, a substantial increase. The area is bounded on the north by cropland and the south by riparian/sand sage habitat. The Cimarron is separated from the Comanche by sand sage habitat unsuitable for black-tailed prairie dog expansion (Shively pers comm. 2008).

Comanche National Grassland; Carizzo Unit: Recent GIS analyses identified 46,395 ha of potential black-tailed prairie dog habitat on this site. Potential habitat was defined as land with clay or loamy soil and <5% slope. Of this potential habitat, 5,627 ha were occupied in 2005. Occupied area in 2007 was 1,439 ha after several years of plague. The Carizzo Unit has extremely fragmented land ownership. Private and federal lands are intermingled. The amount of occupied habitat on intermingled private lands is unknown (Shively pers comm. 2008).

Comanche National Grassland; Timpas Unit: Black-tailed prairie dogs occupy this site on the Timpas Unit, which overlaps on the adjoining U.S. Army Pinon Canyon Maneuvers Site. The Timpas Unit includes a number of private in-holdings but is far less fragmented than the Carizzo Unit (above). The amount of occupied habitat in the Timpas Unit is lower than in the past due to plague. A total of 35,917 ha of potential habitat exist of which 233 ha were occupied in 2003, and 435 in 2007 (Shively pers comm. 2008).

Pawnee National Grassland: Black-tailed prairie dogs occupy a mixture of private and federal land. Prairie dogs occupied 1,013 ha in 62 colonies in 2007. Potential suitable habitat is 12,353 ha. There was an extensive plague outbreak in 2007-2008. Pawnee National Grassland developed a prairie dog management plan in 2006 which included black-footed ferret reintroduction options (Humphrey pers comm. 2008).

Pinyon Canyon Maneuvers Site: Black-tailed prairie dogs occupy this site on the U.S. Army Pinyon Canyon Maneuvers Site adjacent to the Timpas Unit of Comanche National Grassland. About 20 colonies occupied 405 ha in 2007, with recent population fluctuation between 284 and 486 ha. Potential habitat is approximately 39,690 ha of shortgrass prairie (Klavetter pers comm. 2008).

Pueblo Army Depot: Black-tailed prairie dogs currently occupy approximately 486 ha at this site, which is on a U.S. Army installation. Approximately 1,066 ha of occupied habitat were present before a plague outbreak in 2003 (Canestorp pers comm. 2008) and plague was still present in 2006 when 1097 ha were mapped (Young 2008). Estimate of potential habitat is 2,223 ha. The site is protected from shooting and poisoning except where black-tailed prairie dogs may constitute a human health hazard (Woodson pers comm. 2003). A large area of occupied habitat also occurs on private lands adjacent to Pueblo Army Depot in El Paso County (EDAW Inc. 2000; Colorado Division of Wildlife 2003a; Canestorp pers comm. 2008).

Rocky Mountain Arsenal: Black-tailed prairie dogs occupy more than 607.5 ha at present. There are a total of 2,025 ha of potential so expansion is possible. Limiting factors include the fact that the site is bordered by urban development and is adjacent to Denver International Airport and several highways run along the boundary (Hastings pers comm. 2008).

Gunnison's Prairie Dog

BLM Twin Lakes Allotment: Gunnison's prairie dogs occur at this site on public land in Conejos County, approximately 32 km south of Alamosa. The area supports a large complex of colonies dating back to 1970's, many of which are old or inactive. Existing occupied habitat is approximately 512 ha (Albee pers comm. 2003).

Parlin: Gunnison's prairie dogs occur at this site, which is on public land 19 km southeast of Gunnison in Gunnison County. The amount of occupied habitat in 1980 was 497 ha (Albee, pers comm. 2003).

White-tailed Prairie Dog

The Colorado Division of Wildlife conducted a statewide effort in 2003 to document occupied white-tailed prairie dog habitat by interviewing field personnel from the Colorado Division of Wildlife, the U. S. Fish and Wildlife Service and BLM (Colorado Division of Wildlife 2003b). A total of 77,648 ha of active and 19,021 ha of unknown white-tailed prairie dog colonies were documented.

Northwest Moffat County:

Southern Moffat and northern Rio Blanco counties contain the majority of habitat. White-tailed prairie dogs were mapped by White River Field Office in Meeker in 1985 (Hollowed BLM pers comm. in Seglund et al. 2004). These surveys indicated that about 16,000 ha (39,536 ac) of occupied habitat occurred south of US State Highway 40, and north and east of US State Highway 64 in Moffat and Rio Blanco counties (Seglund et al. 2004). These counties might support sites other than Wolf Creek within 3-10 years.

KANSAS

Black-tailed prairie dogs occur in Kansas. Recent black-tailed prairie dog surveys estimate 52,861 ha of occupied habitat in western Kansas (Kansas Black-tailed Prairie Dog Working Group 2002).

Active Sites

Logan County Complex: Smoky Valley Ranch, owned by The Nature Conservancy and 2 private ranches, Barnhardt and Haverfield, are managed as a reintroduction site. Seventeen colonies occur over 3,443 ha of occupied habitat. Most suitable habitat is occupied on the private lands not owned by The Nature Conservancy. Twenty-four black-footed ferrets were released in December 2007. Eight black-footed ferrets were observed during the March 2008 survey (Mulhern pers comm. 2008).

Intermediate Sites

Cheyenne County Complexes: Cheyenne County contains 4 complexes of black-tailed prairie dogs in close proximity, the largest of which is in the northeastern segment of the county northeast of Wheeler, Kansas. It contained 175 ha of black-tailed prairie dogs in 2001. An adjacent complex in central Cheyenne County contained 75 ha and a complex in the northwestern part of the county northwest of St. Francis contained 105 ha. (Kansas Black-tailed Prairie Dog Working Group 2002)

Ford County Complex: Northern Ford County, north of Dodge City, contained a complex of 194 ha of black-tailed prairie dogs in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002)

Greeley County Complex: Northern Greeley County around and north of Tribune, Kansas is a continuous complex of colonies, and along with parts of Wichita, Kearney and Wallace Counties contained the third largest complex (826 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002).

Hamilton County Complex: Western Hamilton County, around Coolidge, Kansas; adjacent to Prowers County, Colorado contained the fifth largest complex (423 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002). This complex and Complex #13 in Colorado (see above) are possibly contiguous.

Hodgeman County Complex: Northeastern Hodgeman County north of Gray, Kansas contained a complex of 144 ha of black-tailed prairie dogs in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002)

Kearney County North Complex: The central part of this county, centered on Lakin, Kansas contained the second largest complex (1,104 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002). It is contiguous with complexes to the north (Wichita County) and south (Kearney County South).

Kearney County South Complex: The southern part of this county, south of Lakin, Kansas, and extending into Grant County, possibly Hamilton and Stanton Counties as well, contained a complex of 400 ha of black-tailed prairie dogs in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002).

Kiowa, Comanche, Clark County Complex: A complex of 109 ha of black-tailed prairie dogs occurred at the junction of the three counties northeast of Coldwater, Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002). This complex in south central Kansas is at least 25 miles from the next closest complex (central Ford County).

Logan, Sherman County Complex: Much of Logan county is a contiguous complex, and extends into several adjacent county, most notably Sherman County. Sherman County had the highest number of colonies and highest occupied area in the 1990-92 survey - 60 colonies and 1,420 ha (Vanderhoof and Robel 1992; 1994). The 3,522 ha Logan/Sherman County Complex includes portions of Gore, Scott, Wichita, Wallace, and Thomas Counties. This was the largest complex of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002).

Rawlins County Complex: This central and northern portion of this county around, north and west of Atwood, Kansas contained the fourth largest complex (448 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002). The complex is contiguous with the Thomas County Complex (see below).

Scott County Complex: West central Scott County near Modoc, Kansas contained a complex of 167 ha of black-tailed prairie dogs in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002)

Stevens County Complex: Stevens county along the Oklahoma border contained three complexes of black-tailed prairie dogs totaling 264 ha of black-tailed prairie dogs in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002). The largest complex south of Moscow, Kansas contained 131 ha, and a second complex north of there contained 114 ha and extended into Grant County.

Thomas County Complex: The northeastern quarter of this county, east of Colby, and extending into Sheridan and Rawlins Counties, possibly connecting with the Rawlins County Complex (see above) contained a complex of 302 ha of black-tailed prairie dogs in 2001 (Kansas Black-tailed Prairie Dog Working Group 2002).

Other Sites

Z-Bar Ranch: Black-tailed prairie dogs occupy this site, which is on property owned by the Turner Endangered Species Foundation approximately 40 km southwest of Medicine Lodge in Barber County. The site is near the eastern edge of the historic black-tailed prairie dog range and was originally mixed grass prairie (Steinauer and Collins 1996), making it a unique area for potential black-footed ferret reintroduction. The site currently supports approximately 100 ha of prairie dogs (Truett pers comm. 2008).

MONTANA

Both black-tailed and white-tailed prairie dogs occur in Montana. White-tailed prairie dogs are confined to a very small area near the border with Wyoming and occupy roughly 40 ha of habitat at the present time therefore no black-footed ferret reintroduction potential exists for the foreseeable future. Black-tailed prairie dogs occur in the eastern part of the state, and the best estimate of occupied area is 36,450 ha (Montana Prairie Dog Working Group 2002).

Active Sites

UL Bend National Wildlife Refuge

Black-tailed prairie dogs occupy approximately 1,300 ha at this site in central Phillips County. Black-footed ferret reintroduction occurred from 1994 until 2005. The area was heavily impacted by plague beginning in 2007, the first time the disease has been documented on the complex. Two-hundred twenty-nine black-footed ferrets were released over 12 years. Only 6 black-footed ferrets were left in the wild in April 2008 (Matchett pers comm. 2008).

BLM-40 Complex

Black-tailed prairie dogs occupied approximately 486 ha at this site in north central Phillips County in 2001, decreasing to 243 ha by 2007. Black-footed ferret reintroduction occurred from 2001 until 2004. The area was heavily impacted by plague beginning in 2005 and continuing into 2007. Ninety-five black-footed ferrets were released over 4 years. No black-footed ferrets were left in the wild by fall 2006 (Matchett pers comm. 2008).

Ft. Belknap Indian Reservation: Black-tailed prairie dogs occupied approximately 5,457 ha at this site in northern Phillips County in the late 1990’s. Black-footed ferret reintroduction occurred from 1997 until 2000. The area was heavily impacted by plague beginning in 2000 and continuing into 2007. One-hundred sixty-seven black-footed ferrets were released over 4 years. No black-footed ferrets were left in the wild by fall 2001 (Matchett pers comm. 2008).

Northern Cheyenne Indian Reservation: The Northern Cheyenne reintroduction complex is in Rosebud County, south-central Montana and contained 126 colonies in two subcomplexes of 1,733 ha and 286 ha, respectively, totaling 2,295 ha in 2006. Approximately 158,700 ha are suitable for livestock grazing, although the area has not all been characterized as potential prairie dog. Prairie dog distribution on Reservation is primarily on the eastern 1/3 of the Reservation associated with the benches and bottomlands along the Tongue River and its tributaries. The Northern Cheyenne Tribe requested, and was approved in 2007 to receive a total of 60 black-footed ferret kits (captive-reared, wild born or a combination) for the initial re-establishment of black-footed ferrets. Four female and four male black-footed ferrets pre-conditioned at Vermejo Park, New Mexico were released on January 24, 2008 as part of that allocation (Northern Cheyenne Indian Reservation 2008).

Intermediate Potential Sites

The following locations were identified in the Conservation Plan for Black-tailed and White-tailed Prairie Dogs in Montana (Montana Prairie Dog Working Group 2002) as the largest prairie dog complexes in Montana in 2000.

Big Sandy: Black-tailed prairie dogs occupy this site west of Havre. The complex contained 236 ha of occupied habitat on a mixture of state, private, and BLM land in the 1990's (Montana Prairie Dog Working Group 2002).

Custer Creek: Black-tailed prairie dogs occupy this site in Prairie and Custer Counties which contained >100 colonies and 2,430 ha of occupied habitat on a mixture of private and BLM land in the 1990's (Montana Prairie Dog Working Group 2002). Plague has not been documented since 1996. Since this site is in an area of checkerboard land status, private interests control the site potential (Lockhart 1998-2007).

Fergus and Petroleum Counties: Black-tailed prairie dogs occupy this site northeast of Lewistown. The complex contained 388 ha of occupied habitat on a mixture of Fish and Wildlife Service and BLM land in the 1990's (Montana Prairie Dog Working Group 2002).

Ingomar: Black-tailed prairie dogs occupy this site in Garfield County northwest of Miles City. The complex contained 1,169 ha of occupied habitat on a mixture of private and BLM land in the 1990's (Montana Prairie Dog Working Group 2002).

Leachman Complex (Crow Reservation): This site is entirely on Tribal land in the northwest portion of the Crow Indian Reservation in Yellowstone and Big Horn counties, and once supported an estimated 4,050-4,860 ha of occupied prairie dog habitat (Montana Prairie Dog Working Group 2002). The site included >2,835 ha of occupied prairie dog habitat in recent times, but suffered a plague outbreak prior to 2003. Approximately 2,430 ha remained in 2 colonies in the southwest and central portions of the area in 2003 (Hanebury pers comm. 2008). Surveys of suitable habitat on the Crow Reservation have not been completed so sites other than the Leachman site may also exist (Hanebury pers comm. 2008).

Lower Tongue River: Black-tailed prairie dogs occupy this site in Custer County south of Miles City. The complex contained 944 ha of occupied habitat on a mixture of private and BLM land in the 1990's (Montana Prairie Dog Working Group 2002).

Upper Musselshell: Black-tailed prairie dogs occupy this site in Petroleum County east of Lewistown. The complex contained 2,672 ha of occupied habitat on a mixture of Fish and Wildlife Service, private, and BLM land in the 1990's (Montana Prairie Dog Working Group 2002).

Upper Tongue River: Black-tailed prairie dogs occupy this site in Rosebud County south of Miles City. The complex contained 475 ha of occupied habitat on a mixture of private and tribal land in the 1990's (Montana Prairie Dog Working Group 2002).

Valley County: Black-tailed prairie dogs occupy this site in Valley County near Glasgow. The complex contained 590 ha of occupied habitat on a mixture of private and BLM land in the 1990's (Montana Prairie Dog Working Group 2002).

NEBRASKA

Only black-tailed prairie dogs occur in Nebraska. Recent surveys estimate 55,481 ha of occupied habitat (Bischof et al. 2004). The 6 counties (Box Butte, Cheyenne, Deuel, Morrill, Scotts Bluff, and Sioux) with the largest amount of occupied area per county occur in the Panhandle and include 30,077 ha of active colonies. Data on location of complexes has not been compiled (Fritz pers comm. 2008). Without identification of complexes, I list all counties which meet my minimum criteria for occupied area (>607.5 ha of colonies) since the potential exists that all of the occupied area in a county may occur in one colony or complex.

Intermediate Potential Sites

Box Butte County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 4,052 ha of active prairie dog colonies in this county north and west of Alliance, Nebraska (Bischof et al. 2004).

Buffalo County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 1,038 ha of active prairie dog colonies in this county (Bischof et al. 2004). Kearney, Nebraska occurs in this county.

Chase County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 2,101 ha of active prairie dog colonies in this county which adjoins Dundy County (Bischof et al. 2004). Imperial, Nebraska occurs in this county.

Cheyenne County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 3,580 ha of active prairie dog colonies in this county which adjoins Deuel and Morrill Counties (Bischof et al. 2004). Sydney, Nebraska occurs in this county.

Custer County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 2,097 ha of active prairie dog colonies in this county (Bischof et al. 2004). The county is near the eastern edge of the historic black-tailed prairie dog range and was originally tallgrass prairie (Steinauer and Collins 1996), making it a unique area for potential black-footed ferret reintroduction. Broken Bow, Nebraska occurs in this county.

Dawes County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 1,194 ha of active prairie dog colonies in this county which adjoins Sioux and Box Butte Counties (Bischof et al. 2004). Chadron, Nebraska occurs in this county.

Dawson County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 1,294 ha of active prairie dog colonies in this county (Bischof et al. 2004). Lexington, Nebraska occurs in this county.

Deuel County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 4,724 ha of active prairie dog colonies in this county containing the town of Chappell, Nebraska and adjoining Sedgwick County, Colorado (Bischof et al. 2004) which contained 767 ha of prairie dog colonies in 2002 (Colorado Division of Wildlife 2003a).

Dundy County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 2,722 ha of active prairie dog colonies in this county which is adjoins Colorado and Kansas in far southwestern Nebraska (Bischof et al. 2004). A 448 ha complex of prairie dogs occurs along the Kansas-Nebraska border in Rawlins County, Kansas. Benkelman, Nebraska occurs in this county.

Frontier County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 725 ha of active prairie dog colonies in this county (Bischof et al. 2004). Curtis, Nebraska occurs in this county.

Furnas County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 849 ha of active prairie dog colonies in this county which adjoins Frontier County and the Kansas border (Bischof et al. 2004). Arapahoe, Nebraska occurs in this county.

Greeley County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 724 ha of active prairie dog colonies in this county (Bischof et al. 2004). The county is at the far eastern edge of the historic black-tailed prairie dog range and was originally tallgrass prairie (Steinauer and Collins 1996), making it a unique area for potential black-footed ferret reintroduction. Greeley, Nebraska occurs in this county.

Harlan County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 1,542 ha of active prairie dog colonies in this county which adjoins the Kansas border (Bischof et al. 2004). Alma Nebraska occurs in this county. A complex of 79 ha occurs along the Kansas-Nebraska border in Phillips County, Kansas.

Hayes County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 1,205 ha of active prairie dog colonies in this county which is adjoins Chase, Frontier, and Hitchcock Counties (Bischof et al. 2004). Hayes Center, Nebraska occurs in this county.

Hitchcock County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 796 ha of active prairie dog colonies in this county which is adjoins Chase, Dundy, Frontier, and Hayes Counties in southwestern Nebraska (Bischof et al. 2004). Trenton, Nebraska occurs in this county.

Keith County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 1,201 ha of active prairie dog colonies in this county which is adjoins Deuel and Perkins Counties (Bischof et al. 2004). Ogallala, Nebraska occurs in this county.

Lincoln County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 1,879 ha of active prairie dog colonies in this county which is adjoins several other counties with active prairie dog colonies (Bischof et al. 2004). North Platte, Nebraska occurs in this county.

Morrill County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 7,290 ha of active prairie dog colonies in this county which is adjoins Box Butte and Scottsbluff Counties (Bischof et al. 2004). Bayard, Nebraska occurs in this county.

Perkins County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 866 ha of active prairie dog colonies in this county which is adjoins several counties with active prairie dog colonies (Bischof et al. 2004). Grant, Nebraska occurs in this county.

Red Willow County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 1,257 ha of active prairie dog colonies in this county which is adjoins several counties with active prairie dog colonies (Bischof et al. 2004). McCook, Nebraska occurs in this county.

Sherman County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 985 ha of active prairie dog colonies in this county (Bischof et al. 2004). The county is near the eastern edge of the historic black-tailed prairie dog range and was originally tallgrass prairie (Steinauer and Collins 1996), making it a unique area for potential black-footed ferret reintroduction. Loup City, Nebraska occurs in this county.

Scotts Bluff County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 7,249 ha of active prairie dog colonies in this county which is adjoins Box Butte and Morrill Counties (Bischof et al. 2004). Scottsbluff, Nebraska occurs in this county.

Sioux County: Surveys conducted by the Nebraska Game and Parks Commission in 2003 identified 3,182 ha of active prairie dog colonies in this county which is adjoins Box Butte and Scottsbluff Counties (Bischof et al. 2004). Harrison, Nebraska occurs in this county.

Other Sites

Blue Creek Ranch: This site, which is owned by the Turner Endangered Species Foundation, is 16 km northeast of Oshkosh in Garden County and currently has only a few ha of occupied habitat. Grassland conservation and black-tailed prairie dog expansion are not high management priorities at present (Truett pers comm. 2008).

Oglala National Grasslands: This site is located in Sioux and Dawes Counties and had 284 ha of occupied black-tailed prairie dog habitat in 2003. The Oglala National Grassland may be able to consolidate the land base and expand existing prairie dog habitat to accommodate black-footed ferrets within 10 years (Larson pers comm. 2008).

NEW MEXICO

Black-tailed and Gunnison's prairie dogs occur in New Mexico. Recent black-tailed prairie dog surveys estimate 24,300 ha of occupied habitat (Johnson et al. 2003) in eastern New Mexico. Johnson et al. (2003) identified 2 complexes >2,025 ha, 5 complexes between 405 and 2,025 ha, and 20 complexes <405 ha. Surveys are ongoing for Gunnison's prairie dog but there is no estimate of current occupied habitat.

Active Sites

Vermejo Park Ranch: The site, which is owned by the Turner Endangered Species Foundation, is located 40 km southwest of Raton and has grown from 200 ha of occupied habitat in 1997 to 2,025 ha in 2008. Potential habitat is 4,050 ha. Prairie dogs are still rapidly expanding into suitable habitat. The site has been used as a black-footed ferret nursery colony since 2005, but in 2008 black-footed ferrets will be left on site to determine whether a self-sustaining population can be established. Grassland conservation and black-tailed prairie dog expansion are high priorities (D. Long, written comm. 2008).

Intermediate Potential Sites

Gunnison's Prairie Dog

Chavez Ranch: Gunnison's prairie dogs have occurred at this site for greater than 50 years (Chavez Ranch pers comm. 2005). Landownership is a mixture of state, BLM, and private land. Occupied area is approximately 486 ha (Luce 2005b).

Frenches Draw: This Gunnison's prairie dog complex occurs on state land approximately 20 miles northwest of Quemado, New Mexico. Prairie dogs contiguously occur at low density over approximately 1,013 ha (Luce 2005b). Individual colonies were not mapped. Prairie dogs are reported to have occurred over several thousand ha in 1960's but occupied area and colony are unknown due to lack of mapping.

Johnson Basin: The U.S. Forest service mapped 30 ha of prairie dogs in 1983 (Morrison pers comm. 2005). Mapping in 2005 indicated 151 occupied ha, encompassing and exceeding the 1983 occupied area. Inactive burrows occurred on the periphery of the colony indicating some recession in the recent past (Luce 2005b).

Black-tailed Prairie Dog

Lea County: The site is northeast of Lovington and contains approximately 9,720 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 60 ha, and the maximum area of a single colony is 956 ha (Johnson et al. 2003).

Quay/Curry County Interface: The site is south of Tucumcari and contains >3,848 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 19 ha, and the maximum area of a single colony is 152 ha. (Johnson et al. 2003)

Roosevelt County: The site is south of Portales and contains >5,265 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 35 ha, and the maximum size of a single colony is 339 ha (Johnson et al. 2003).

Union County: This site is southwest of Clayton and contains approximately 3,240 ha of occupied habitat. The mean size of colonies is 41 ha, and the maximum area of a single colony is 292 ha (Johnson et al. 2003).

NORTH DAKOTA

Only black-tailed prairie dogs occur in North Dakota. A 2003 survey estimated 8,130 ha of occupied habitat in western North Dakota (Knowles 2003).

Intermediate Potential Sites

Northwest McKenzie Complex, Little Missouri National Grassland: This site is in McKenzie County in western North Dakota. Black-tailed prairie dogs occupied 238 ha in 1997, 303 ha in 2002 and 419 ha in 34 colonies in 2005 (Svingen 2006b). Mapping planned for 2008 will very likely show a further increase in occupied area (Svingen pers comm. 2008).The Little Missouri National Grassland Grasslands Plan includes black-footed ferret objectives. The area is plague free (Svingen pers comm. 2008).

Southwest McKenzie Complex, Little Missouri National Grassland: This site is in McKenzie County in western North Dakota. Black-tailed prairie dogs occupied 97 ha in 1997, 175 ha in

2002 and 323 ha in 12 colonies in 2005 (Svingen 2006b). Mapping planned for 2008 will very likely show a further increase in occupied area (Svingen pers comm. 2008). The Little Missouri National Grassland Grasslands Plan includes black-footed ferret objectives. The area is plague free (Svingen pers comm. 2008)

Northeast Slope County, Little Missouri National Grassland: This site is in Slope County near the Montana border. The U.S. Forest Service identified a prairie dog focal area northeast of Marmath, North Dakota which contained 68 ha of occupied prairie dog habitat on a mixture of federal and private land in 2005 (Svingen 2006).

Southwest Slope County, Little Missouri National Grassland: This site is in Slope County along the Montana border. The U.S. Forest Service identified a prairie dog focal area north of Marmath, North Dakota that contained 469 ha of occupied area on a mixture of federal and private land in 2005 (Svingen 2006). This site has the most potential for black-footed ferret reintroduction on Little Missouri National Grassland at present (Svingen pers comm. 2008).

Standing Rock Complex (Standing Rock Indian Reservation and adjacent lands): Black-tailed prairie dogs occupied 3,651 ha in 224 colonies at this site in Sioux County in 2002 (Knowles 2007). In 2006, 264 colonies occupied 3,995 ha (Knowles 2007). Colonies are scattered over a large area, and the land base is a checkerboard of private and tribal lands. The area is plague free (Knowles 2007).

South Unit Theodore Roosevelt National Park: Black-tailed prairie dogs occupied 628 ha in 25 colonies at this site in Billings County in 2007. Roughly 486 ha, the majority of colonies on the Park, are grouped in a complex along the Little Missouri River, while approximately 120 ha occur near the far eastern boundary of the Park. In 2002, 61 active colonies were mapped on the Park (Knowles, 2003) so decline has occurred. Knowles (2003) predicts that the site potential on the National Park is >2,633 occupied ha based on the amount of suitable habitat present. Additional suitable habitat occurs on adjacent private and U.S. Forest Service land. The area is plague free (Oehler pers comm. 2008; Knowles 2003)

Little Missouri River Complex: Black-tailed prairie dogs occupy several sites in Slope County. The site broadly described as Little Missouri River Complex includes specific sites (see Northeast Slope County and Southwest Slope County, Little Missouri National Grassland above) but I include it separately in this analysis to illustrate that with private landowner participation a very significant land area in the plague free zone could be dedicated to black-footed ferret recovery. The site had 316 colonies over 4,479 ha in 2002, increasing to 343 colonies over 5,064 ha in 2006 (Knowles 2007).

OKLAHOMA

Only black-tailed prairie dogs occur in Oklahoma. Aerial surveys estimated 26,007 ha of occupied habitat in 2002 in western Oklahoma (Hoagland pers comm. 2003).

Intermediate Potential Sites

The three Panhandle Counties of Beaver, Texas, and Cimarron support an almost continuous prairie dog complex (complex defined as a group of colonies no more than 7 Km from another colony) (Weimers pers comm. 2008). In addition, the complexes adjoin those described for the State of Texas where the two states border (see below).

Beaver County #1: This site is in the east central part of the county. Cluster E had 10 colonies with a total of 93 ha when mapped in 1996-98 (98 (Lomolino pers comm. 2003, Lomolino and Smith 2001).

Beaver County #2: This site is in the south-central part of the county. Cluster F had 34 colonies with a total of 319 ha when mapped in 1996-98 (Lomolino pers comm. 2003, Lomolino and Smith 2001).

Cimarron County: This site is in the southwestern corner of the county. Cluster A had 12 colonies totaling 345 ha and Cluster B had 6 colonies with a total of 652 ha when mapped in 1996-98 (Lomolino pers comm. 2003, Lomolino and Smith 2001).

Texas County #1: This site is in the north central part of the county. Cluster C had 12 colonies with a total of 332 ha when mapped in 1996-98 (Lomolino pers comm. 2003, Lomolino and Smith 2001).

Texas County #2: This site is in the east central part of the county. Cluster D had 18 colonies with a total of 302 ha when mapped in 1996-98 98 (Lomolino pers comm. 2003, Lomolino and Smith 2001).

SOUTH DAKOTA

Only black-tailed prairie dogs occur in South Dakota. The 2006 survey estimated 253,291 ha of occupied habitat in western South Dakota of which 220,492 ha occur in 2 high density areas (Kempema 2007). Of this, 91,912 ha occur on non-tribal land and 128,579 ha occur on tribal land (Kempema 2007). Much of the non-tribal occupied area is in counties with a significant amount of federal land, therefore prairie dog concentration areas which are potential black-footed ferret reintroduction sites are identified by the federal land holding rather than by county except where counties are specifically named as Intermediate Sites.

Active Sites

Badlands National Park: Black-tailed prairie dogs occupy this site in Pennington, Shannon, and Jackson Counties. Total occupied habitat is 1,337 ha within 98,820 ha of public land. There are 2,633 ha of suitable habitat for expansion. The black-footed ferret population was 22 in fall 2007 (Larson pers comm. 2008).

Cheyenne River Sioux Reservation: Black-tailed prairie dogs occupy this site in Dewey and

Zeibach Counties. Plague is present on the Reservation but not at the reintroduction site at this time. Total occupied habitat is 17,861 ha in three separate complexes, one of which is 8,424 ha (Lockhart 1998-2007). Black-footed ferrets occur over 3,888 ha of prairie dog colonies. The first black-footed ferret releases occurred in 2000 at the East Moreau River Complex. Twenty black-footed ferrets were translocated in 2006 to Lower Brule and Rosebud Sioux reintroduction sites. Current population estimate is 110 black-footed ferrets (Larson pers comm. 2008).

Conata Basin: Black-tailed prairie dogs occupy this site in Pennington, Shannon, and Jackson Counties. Total occupied habitat is 12,150 ha within 30,375 ha of public land. There is little suitable habitat for expansion. Recent plague events have impacted at least 3,280 ha. The black-footed ferret population was 290 in the fall 2007 (Larson pers comm. 2008).

Lower Brule Sioux Reservation: Black-tailed prairie dogs occupy 1,701 ha at this site in Stanley and Lyman Counties. Potential habitat far exceeds occupied habitat. Black-footed ferrets were released on a complex of about 648 ha in the southeast corner of the Reservation in 2006. Recent surveys have documented 12 extant black-footed ferrets (Larson pers comm. 2008).

Rosebud Sioux Reservation: Black-tailed prairie dogs occupy 28,350 ha at this site in Todd and Mellette Counties, 18,225 ha of which is on tribal trust lands (Lockhart 1998-2007). Two prairie dog complexes, Iron Shell Flats and Lower Cut Meat, were identified for black-footed ferret releases. Releases occurred on 1,012 ha of prairie dog colonies at Iron Shell Flats Complex in 2004. The black-footed ferret population has been stable at about 30 (Larson pers comm. 2008).

Wind Cave National Park: Black-tailed prairie dogs occupy 689 ha at this site in Custer County. All prairie dogs are in one contiguous complex. Black-footed ferret releases began in 2007. Surveys conducted in 2007 found 18 extant black-footed ferrets (Larson pers comm. 2008).

Intermediate Potential Sites

Corson County: Corson County has 7,733 ha of prairie dog colonies, 68% on private land (Kempema 2007) and not part of an active complex. Southwest Corson County contained a complex of 242 ha of colonies on the U. S. Forest Service's Grand River National Grassland in 2005 (Svingen 2004).

Custer County: Custer County has 7,669 ha of prairie dog colonies, 39% on private land (Kempema 2007) and not part of an active complex.

Dewey County: Dewey County has 6,950 ha of prairie dog colonies on private land (Kempema 2007) and not part of an active complex.

Fall River County: Fall River County has 6,826 ha of prairie dog colonies, 73% on private land (Kempema 2007) and not part of an active complex.

Jackson County: Northern Jackson County (off Reservation) has 6,384 ha of prairie dog colonies, 84% on private land (Kempema 2007) and not part of an active complex.

Ziebach County: Ziebach County (off Reservation) adjoining Cheyenne River Indian Reservation has 5,020 ha of prairie dog colonies, 89% private land (Kempema 2007) and not part of an active complex.

Other Sites

Bad River Ranch: Black-tailed prairie dogs occupy this site on lands owned by Turner Endangered Species Foundation in Stanley and Jones counties, 16 km southwest of Pierre. The site has over 500 ha of occupied habitat and is growing steadily. Grassland conservation and black-tailed prairie dog expansion are high priorities. There is no history of plague in the area (Truett pers comm. 2008).

Ft. Pierre National Grassland: This National Grassland is located in Jones, Lyman, and Stanley Counties. Approximately 729 ha of plague free black-tailed prairie dogs currently occur within 46,980 ha of National Grasslands, 41,812 ha of which is suitable prairie dog habitat. The area adjoins Lower Brule Sioux Indian Reservation; however black-footed ferret releases begun on the Reservation in 2006 were not adjacent to the Grasslands (Larson pers comm. 2008).

Grand River National Grassland: Black-tailed prairie dogs currently occupy 850 ha at this site in Perkins and Corson Counties. In the current land management plan the U.S. Forest Service has designated 3 focal areas and will manage to retain 2 or more prairie dog complexes. Prairie dog expansion will be encouraged. There are over 50,000 ha of suitable habitat on the National Grassland. There is no history of plague in the area (Svingen pers comm. 2008; Larson pers comm. 2008).

Pine Ridge Indian Reservation: Black-tailed prairie dogs occupied 20,250 – 40,500 ha on tribal lands at this site in Shannon County before plague outbreaks beginning in 2005. The site has the biological capacity to support a large black-footed ferret population (Larson pers comm. 2008).

Smithwick Area, Buffalo Gap National Grassland, Fall River Ranger District: Black-tailed prairie dogs occupy 405 ha at this site in Custer County during earlier surveys, but after plague events in 2005 and 2006 the occupied area is less than 200 ha. Potential habitat is approximately 6,075 ha. The site was included in the most recent land management plan for Buffalo Gap National Grassland (Larson pers comm. 2008).

Standing Rock Indian Reservation: Black-tailed prairie dogs occupy 2,835 ha at this site in Corson County. Black-tailed prairie dog are scattered over a large area, and the land base is a mixture of private and tribal. Both the Reservation and the prairie dog complex extend into adjacent North Dakota. There is no history of plague in the area (Larson, pers comm. 2008).

Triple 7 Ranch: This private ranch in Custer County is approximately 11,340 ha in size and has 1,458 ha of black-tailed prairie dogs. There is some potential to expand the prairie dog occupied area (Larson pers comm. 2008).

TEXAS

Only black-tailed prairie dogs occur in Texas. Recent surveys documented 66,400 ha of occupied habitat in western Texas (Singhurst pers comm. 2008). Data from Ernst (2001) were consulted for comparison. Some counties in Texas may contain several complexes but I did not separate them in this publication.

Intermediate Potential Sites

Surveys completed in 2005 documented the presence of 6 complexes greater than 2.025 ha, 9 complexes between 405 and 2,025 ha, and 4 complexes 324 – 385 ha. Most of the complexes occur over more than one county therefore they are grouped when describing the complex. Complexes were defined as a group of colonies occurring no more than 5 Km from another colony (Singhurst pers comm. 2008).

Complexes >2,025 ha

Bailey, Parmer, Lamb, Cochran, and Hockley Counties: This complex includes an estimated 3,645 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Dallam, Sherman, Hansford, Ochiltree, Hartley, Moore, Potter, Hutchinson and Oldham Counties: This complex includes an estimated 20,250 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Deaf Smith, Parmer, Castro, Swisher, Randall, Oldham, Potter, and Carson Counties: This complex includes an estimated 9,315 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Hudspeth County: This isolated complex includes an estimated 4,860 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Lynn County: This isolated complex includes an estimated 2,025 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Pecos, Crane, Crocker, and Upton Counties: This isolated complex includes an estimated 2,025 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Complexes between 405 and 2,025 ha:

Cochran, Hockley, Yoakum, and Terry Counties: This complex includes an estimated 2,025 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Brewster County: This complex includes an estimated 2,025 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Hockley, Lubbock, Lamb and Hale Counties: This complex includes an estimated 1,620 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Floyd, Hale, Swisher and Briscoe Counties: This complex includes an estimated 810 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Hutchinson, Carson, Gray, and Roberts Counties: This complex includes an estimated 810 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Lipscomb County: This complex includes an estimated 810 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Upton, Reagan, and Glasscock Counties: This complex includes an estimated 405 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Hemphill, Ochiltree, and Lipscomb Counties: This complex includes an estimated 405 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Lipscomb, Hemphill, Wheeler, and Gray Counties: This complex includes an estimated 405 ha of occupied prairie dog colonies. There are several breaks (fault lines) within the complex (Young pers comm. 2008).

Complexes between 324 and 385 ha:

Midland, Upton, Ector Counties: This complex occurs in two large colonies (Young pers comm. 2008).

Lynn, Garza, Borden Counties: This complex occurs in three large colonies (Young pers comm. 2008).

Yoakum and Gaines Counties: This complex occurs in three large colonies (Young pers comm. 2008).

Hale County: This complex occurs in one large colony (Young pers comm. 2008).

Other Sites

Muleshoe National Wildlife Refuge, Bailey County: Black-tailed prairie dogs occupy this site northwest of Lubbock. Prairie dogs are recovering from a plague outbreak in the 1980's and occupied area is approximately 20 ha (Beierman pers comm. 2008). This site occurs within the 3,645 ha Bailey, Parmer, Lamb, Cochran, and Hockley County Complex.

Rita Blanca National Grassland/northern Dallam County: Black-tailed prairie dogs occupy this site north of Dalhart. Prairie dogs are recovering from a plague outbreak in the 1980's and occupied area is small at present (Garcia pers comm. 2008). The National Grassland occurs with the Dallam, Sherman, Hansford, Ochiltree, Hartley, Moore, Potter, Hutchinson and Oldham County Complex.

UTAH

Gunnison's prairie dogs occur in extreme southeastern Utah and white-tailed prairie dogs occur in northeastern Utah.

Active Sites

Coyote Basin: White-tailed prairie dogs occupy this site in northeastern Utah in Uinta and Grand Counties along the Colorado border (Moffat and Rio Blanco Counties) and Wyoming (Sweetwater and Uinta Counties) border. The complex may extend into both Utah and Wyoming. Reintroduction efforts began in 1999, with 200 black-footed ferrets released to date. Releases are ongoing. A minimum of 25 black-footed ferrets occur in the wild at present. Forty-four colonies were present in 1997-98 on 7,604 ha, primarily on BLM land. Plague is present. Potential habitat is significantly greater than occupied area (Lockhart 1998-2007).

Intermediate Potential Sites

Buckhorn: White-tailed prairie dogs occupy this site in Emery County in south eastern Utah. Cedar Creek Associates mapped 2,684 ha in 11 colonies in this complex on public lands in 1985. In 2002, the area contained 3,739 ha in 3 large colonies. The primary area of occupation is just west of Green River, Utah, but prairie dog colonies extend roughly 60 miles to the southwestern corner of the county (Seglund et al. 2004).

Cisco Desert: This site in Grand County has been identified by the black-footed ferret recovery program as having near-term potential for reintroduction. White-tailed prairie dogs occupied 2,684 ha in 12 colonies at this potential reintroduction site in 2002 (Seglund et al. 2004). Plague is present as shown by the fact that when the site was mapped in 1985 (Boschen 1986) there were 16,729 occupied hectares in 122 colonies. The site is on public land in east central Utah along I-70 from east of Green River to the Colorado border. Landownership is mixed private, state, and federal (Lockhart 1998-2007).

Crescent Junction: White-tailed prairie dogs occupy this site in adjacent to Buckhorn (above). Cedar Creek Associates mapped 4,089 ha in 33 colonies in this complex on public lands in 1985. In 2002, the area contained 3,973 ha in 10 colonies. The occupied area is west of Green River, Utah (Seglund et al. 2004).

Eight Mile Flat (Myton Bench): White-tailed prairie dogs occur at this site on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. Eightmile Flat contained 2,673 ha of occupied habitat in 3 colonies in 1985. The site was resurveyed in 1999 and found to have increased to 2,936 ha of occupied habitat in 24 colonies (Seglund et al. 2004).

Huntington: White-tailed prairie dogs occupy this site in Emery and Carbon Counties). In 1994, 2,352 ha of occupied habitat occurred in 31 colonies. In 2002, the area contained 321 ha in 6 colonies (Seglund et al. 2004).

Kennedy Wash: White-tailed prairie dogs occupy this site in the Uinta Basin. In 1999, survey data estimated 10,697 ha of occupied habitat. In 2003, the area contained 3,313 ha (Seglund et al. 2004).

Rich County: White-tailed prairie dogs occupy this site which is primarily on Deseret Ranch and near the Utah/Wyoming border. Survey data from the 1980's and 2000's both indicated a relatively stable prairie dog population occupying approximately 4,050 ha (R. Danvir pers comm. 2008).

Shiner Basin: White-tailed prairie dogs occupy this site in the Uinta Basin. In 1997, survey data estimated 15,065 ha of occupied habitat. In 2000, the area contained 13,707 ha (Seglund et al. 2004).

Snake John: White-tailed prairie dogs occupy this site in the Uinta Basin. In 2001, survey data estimated 49,346 ha of occupied habitat. In 2003, the area contained 31,118 ha (Seglund et al. 2004).

Sunshine Bench: White-tailed prairie dogs occur at these sites on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. The site was mapped to evaluate suitability for black-footed ferret reintroduction in 1992-93 (Cranney and Day1994). The Sunshine Bench complex contained 2,085 ha of occupied habitat in 7 colonies in 1992-93, while the adjacent Brush Creek area contained 145 ha of occupied habitat. The combined occupied area of Sunshine Bench and Brush Creek was 7,837 ha in 38 colonies in 2002 (Seglund et al. 2004).

Twelve Mile Flat: White-tailed prairie dogs occur at this site on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. Twelvemile Flat contained 363 ha of occupied habitat in 3 colonies in 1985. The site was resurveyed in 1992-93

(Cranney and Day, 1994) and found to have 771 ha of occupied habitat, slightly over double the amount present in 1985. In 2002, 901 ha of occupied habitat occurred in 24 colonies (Seglund et al. 2004).

Woodside: White-tailed prairie dogs occupy this site in Emery and Carbon Counties). In 1985, 871 ha of occupied habitat occurred in 6 colonies. In 2002, the area contained 169 ha in 1 colony (Seglund et al. 2004).

WYOMING

Black-tailed and white-tailed prairie dogs occur in Wyoming. Black-tailed prairie dogs occur in the eastern one-third of the state. The current estimate is 85,168 ha of occupied habitat (Grenier et al. 2004). White-tailed prairie dogs occur in the west central part of the state. A survey conducted in the late 1980's estimated a minimum of 185,988 ha of occupied habitat (Seglund et al. 2004).

Active Sites

Shirley Basin: Shirley Basin/Medicine Bow is in the white-tailed prairie dog range. The site was fully mapped in 1989 (Conway 1989) and again in 1990 using a combination of aerial transects and ground verification (Hnilicka and Luce 1992). In 1990, intensive mapping showed the complex to contain 59,726 ha (Parrish and Luce 1990). Captive-bred black-footed ferrets were released from 1991-94, and the highest number of black-footed ferrets found on subsequent surveys was in 2006, when 192 individuals were located during spotlight surveys. The population is estimated at 229 individuals (161-298, 95% CI) (Grenier 2008*)* within only 20% of the potentially occupied habitat (based on 1990 mapping data). Therefore, considerable potential exists for a large contiguous population of black-footed ferrets, or several sub-populations. It is important to note that prairie dogs have persisted with plague present since at least 1987 (Orabona-Cerovski 1991) and black-footed ferrets since 1991 (Grenier 2008).

Immediate Potential Sites

Saratoga: White-tailed prairie dogs occupy this site around and south and west of Saratoga in Carbon County. Land ownership is a mixture of public and private land. The site had more than 10,000 ha of occupied habitat in 1989 when it was first surveyed (Conway 1989). (Grenier et al. 2003; Grenier 2004) estimated 12,194 ha. The U.S. Fish and Wildlife Service and Wyoming Game and Fish Department are actively working to expand the Shirley Basin Non-essential Experimental Population Area to include Saratoga.

Intermediate Potential Sites

White-tailed Prairie Dog

Bolton Ranch: This site is west of Saratoga in Carbon County. Land ownership is a checkerboard of public and private land. The site had 4,500 ha of occupied habitat in 1989 when it was first surveyed (Conway, 1989). Grenier (2004) estimated 2,718 ha. The U.S. Fish and Wildlife Service and Wyoming Game and Fish Department are actively working to expand the Shirley Basin Non-essential Experimental Population Area to include Bolton Ranch.

Carter: This site is 32 km southeast of Kemmerer, on BLM lands in Lincoln County. The site has not been fully mapped or transected to determine prairie dog density. It contained in excess of 4,050 ha of occupied habitat when partially mapped in the 1980s (Luce pers comm. 1995; Grenier et al. 2003). Grenier (2004) estimated 2,236 ha.

Cumberland: This site is southwest of Kemmerer in Lincoln County. Land ownership is a checkerboard of public and private land. The site was fully mapped and preliminary density data were collected in the 1980s (Clark and Campbell 1981). Occupied habitat was 4,293 ha. Grenier (2004) estimated 9,159 ha.

Fifteen-mile: This site is on BLM land 40 km west of Worland in Hot Springs County. The site contained 3,078 ha of occupied habitat when mapped in the 1980s and has not been remapped (Luce pers comm. 1995; Grenier et al. 2003). Grenier (2004) estimated 4,060 ha.

Flaming Gorge: This site is on BLM land 64 km south of Green River in Sweetwater County. The site was intensively mapped in 1989 and contained 3,049 ha of occupied habitat (Martin and Luce 1990). Grenier (2004) estimated 2,436 ha.

Kinney Rim: This site is southwest of Rawlins on BLM land adjacent to the Wolf Creek Complex in Colorado and is included in the Endangered Species Act of 1973, Section 10(j) Non-essential Experimental Population Designation for Wolf Creek. The site was mapped in the 1980's but has not been fully remapped since that time (Luce pers comm. 1995; Grenier et al. 2003). Grenier (2004) estimated 7,215 ha.

Meeteetse: This site is west of Meeteetse in Park County. This site, from which all of the black-footed ferret captive-breeding stock was taken, had 4,930 ha of occupied habitat in 1982 just after black-footed ferrets were first discovered, and a high population of 129 black-footed ferrets (43 adults, 25 litters) in 1984. Due to plague in white-tailed prairie dogs, occupied habitat was reduced to roughly 2,029 ha by 1989, when all extant black-footed ferrets were captured for captive breeding (Black-footed Ferret Advisory Team 1990). The site has not shown significant recovery of prairie dogs since 1989 (Biggins 2003). The habitat capability of the site remains, including old burrow systems, therefore the potential exists for recovery to sufficient occupied habitat for black-footed ferret reintroduction within 10 years. Grenier (2004) estimated 4,371 ha.

Moxa: The Moxa site, potentially connected to Carter (see above), is 32 km north of Kemmerer. Moxa was identified in the mid-1990s when 17,415 ha of occupied habitat were rough mapped (Luce pers obs. 1995). Grenier (2004) estimated 13,219 ha.

Pathfinder: This site is on federal lands northwest of and adjacent to Shirley Basin Complex in northwest Carbon County. The site was mapped in the 1980's but has not been remapped (Luce pers comm. 1995; Grenier et al. 2003). Grenier (2004) estimated 5,061 ha.

Seminoe: This site is north of Rawlins on BLM land west of the Platte River and adjacent to Shirley Basin Complex. The site was mapped in the 1980's but has not been remapped (Luce pers comm. 1995; Grenier et al. 2003). Grenier (2004) estimated 698 ha.

Shamrock Hills: This site is on BLM land 16 km north of Rawlins in Carbon County. The site was mapped in the 1980's and had >4,050 ha of occupied habitat. The site has not been remapped (Luce pers comm. 1995; Grenier et al. 2003). Grenier (2004) estimated 8,005 ha.

Sweetwater: This site is on BLM land 30 miles southeast of Lander in Fremont County. The site was mapped in the 1980's (Luce pers comm. 1995; Grenier et al. 2003) and remapped in 2002 (Grenier 2004a). Grenier (2004) estimated 5,752 ha.

Black-tailed Prairie Dog

Arvada: This site is near the town of Arvada at the juncture of Campbell, Johnson, and Sheridan Counties. The area is mixed ownership. Six hundred seventy-three colonies occurred over 14,835 ha of suitable habitat in 2003 (Grenier et al. 2004).

Bill East: This site is west of Lance Creek along the Converse- Niobrara County line. The area is mixed ownership. Twenty-one colonies occurred over 442 ha of suitable habitat in 2003 (Grenier et al. 2004).

Casper North: This site is north of the City of Casper. The area is mixed ownership. Twelve colonies occurred over 2,273 ha of suitable habitat in 2003 (Grenier et al. 2004).

Casper South: This site is south of the City of Casper. The area is mixed ownership. Fifty-nine occurred over 3,985 ha of suitable habitat in 2003 (Grenier et al. 2004).

Four Corners: Black-tailed prairie dogs occupy this site north of the town of Kaycee in Johnson County. The area is mixed ownership. Twenty-nine colonies occurred over 1,754 ha of suitable habitat in 2003 (Grenier et al. 2004).

Kaycee: This site is west of the town of Kaycee in Johnson County. The area is mixed ownership. Thirty colonies occurred over 2,458 ha of suitable habitat in 2003 (Grenier et al. 2004).

Linch: This site is in southeastern Johnson County. The area is mixed ownership. Fifty-seven colonies occurred over 1,830 ha of suitable habitat in 2003 (Grenier et al. 2004).

Moorcroft: This site is south of Sundance in Crook County. The area is mixed ownership. Twenty-three colonies occurred over 574 ha of suitable habitat in 2003 (Grenier et al. 2004).

Pleasantdale: This site is west of the town of Gillette in Campbell County. The area is mixed ownership. Seventy-one colonies occurred over 969 ha of suitable habitat in 2003 (Grenier et al. 2004).

Ross: This site is east of the town of Edgerton in northwest Converse County. The area is mixed ownership. Twenty colonies occurred over 1,400 ha of suitable habitat in 2003 (Grenier et al. 2004).

Slater: This site is west of the town of Torrington in Goshen County. The area is mixed ownership. Twenty-nine colonies occurred over 792 ha of suitable habitat in 2003 (Grenier et al. 2004).

Torrington: This site is near the town of Torrington in Goshen County. The area is mixed ownership. Eighty colonies occurred over 2,092 ha of suitable habitat in 2003 (Grenier et al. 2004).

Other Sites

Sheridan (including National Guard Sheridan Local Training Center): This site is on the U.S. Army installation adjacent to the City of Sheridan in Sheridan County. The site contained 284 ha of occupied black-tailed prairie dog habitat in 2001 (Luce pers obs., 2003). The entire Sheridan Complex contained 127 colonies over 4.054 ha of suitable habitat in 2003 (Grenier et al. 2004).

Thunder Basin National Grassland: This site is in Campbell, Converse, and Weston Counties. The site is identified as a black-footed ferret reintroduction site in the Medicine Bow National Forest/Thunder Basin National Grassland the Forest Plan. There was no history of plague before 2001 when an extensive die-off occurred, reducing occupied habitat by over 4,050 ha. Significant further reduction has occurred since then. Prior to the plague outbreak, occupied black-tailed prairie dog habitat was 8,079 ha, including 7,290 ha on Forest Service lands and 789 ha on state land. The Forest Service estimates that there are 193,590 ha of potential habitat on Forest Service lands (T. Byer pers comm. 2003).

CANADA

Only black-tailed prairie dogs occur in Canada, which is the northern extent of the range of the species. A prairie dog management plan and a black-footed ferret recovery strategy were prepared for Grasslands National Park in 2008. There are no active reintroduction sites in Canada but a black-footed ferret allocation request is being prepared for 2009.

Immediate Potential Sites

Grasslands National Park and vicinity: Black-tailed prairie dogs occur at this site in Saskatchewan, 160 km south of Swift Current. The site had 25 colonies containing a minimum of 1,044 ha in 2002. The number of occupied hectares had remained relatively stable from 1998 to 2002, and is still similar in 2008. There is no plague in the area. (Fargey pers comm. 2008)

MEXICO

Black-tailed prairie dogs occur in northern Mexico, the southern extent of the range, and are the only species of prairie dog in Mexico in the historic range of the black-footed ferret.

Active Sites

Janos: Black-tailed prairie dogs occur at this site 15 Km northwest of Janos in the State of Chihuahua. Estimated occupied prairie dog habitat is 15,000 ha, and the potential suitable habitat is 30,000 ha. Land ownership is divided between ejidos and private. This is a large prairie dog complex and may have the potential for one contiguous black-footed ferret population, or several sub-populations (List pers comm. 2008).

DISCUSSION

The black-footed ferret is a highly specialized prey/habitat obligate of prairie dogs and this dependence has proven catastrophic because of the dramatic reduction of its prey over the past century due to adverse land use practices and disease. Prairie conversion to crop land and poisoning to reduce forage competition with domestic livestock were and continue to be major impacts; while sylvatic plague, an exotic disease catastrophic to prairie dogs, continues to have severe impacts (Cain et al. 1972; Hansen 1988; Cully 1993; Van Pelt 1999; U.S. Fish and Wildlife Service 2000; Cully and Williams 2001; Antolin et al. 2002; Luce 2003).

It is clear from both recent and on-going reintroduction efforts that suitable habitat for black-footed ferret reintroduction and long term population viability at a given site varies widely between sites and prairie dog species. The Recovery Plan (U.S. Fish and Wildlife Service 1988) emphasized the need to establish the broadest possible distribution of black-footed ferrets within the historic range. This approach is important to protect the species from adverse impacts that may occur locally, especially disease, and justifies considering all sites which now meet minimum biological parameters as potential reintroduction sites upon which planning should proceed expeditiously.

Further, and perhaps eventually more important, is initiating at least preliminary planning efforts at sites which do not meet minimum biological parameters now but have a high probability of doing so within 10 years if sufficient planning effort is directed toward the site.

Preparation of this paper does not constitute a proposed state or federal action at any of the proposed sites; it is a conceptual approach to aid in black-footed ferret recovery by identifying potential reintroduction sites at a gross level. Many steps will be required before a site could eventually receive ferrets and myriad actions would be necessary to insure that private land owners, if any, are supportive and involved in the process.

However, I do not believe that it is necessary or appropriate to wait for final biological, social, and political issues to be addressed at a given site in order for it to be on the list of potential reintroduction sites. Therefore, this conceptual exercise identifies sites which either currently have enough prairie dog occupied area to support at least a small black-footed ferret population, or have a small but increasing prairie dog population and sufficient suitable habitat that could support black-footed ferrets within 10 years.

Identification of appropriate sites for black-footed ferret reintroduction has been ongoing for over two decades. The 1988 Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service 1988) set a down listing goal for the species at 1,500 adults in 10 or more populations dispersed across its historic range, with no single population being less than 30 adults. Downlisting the species (move it from Endangered to Threatened status) would not represent complete recovery. Delisting criteria discussed for the 2008 Recovery Plan (U.S. Fish and Wildlife Service in prep. 2008) are likely to require establishment of a population of at least 3,000 breeding adults in 30 or more populations dispersed across the historic range, with no single population being less than 30 breeding adults, and with at least 10 populations with 100 or more breeding adults. It is apparent that removal of the black-footed ferret from the Endangered Species List (pursuant to the Endangered Species Act of 1983, as amended) will require many more than 30 recovery sites due to the transient nature of many sites.

Therefore I suggest that it may be necessary to evaluate and develop a queue of many more than 100 sites across the historic range of the species. These sites should be widely dispersed over the ranges of all 3 prairie dog species and represent the widest variety of habitats, ecological circumstances, disease circumstances, etc. Some sites may prove not to be useable for biological, social or, other reasons, or may not be successful, so concurrent development and occupation of many sites will be necessary.

Plague is a confounding factor. Annual monitoring to document plague activity and the amount of habitat affected would assist prairie dog and black-footed ferret management (Luce 2003). Of course, development of an effective oral vaccine to immunize prairie dogs would assist tremendously. However continuing research on the mechanisms by which plague is spread, usefulness of pre-treatment dusting of prairie dog burrows, and post-treatment dusting of burrows to kill fleas and thus reduce the magnitude of the epizootic may also be practical management tools to combat the disease within the next 10 years. Meanwhile, maintaining both spatial distribution of prairie dog complexes and isolated colonies over the entire range to act as reservoirs to replace prairie dogs lost to plague, and development of black-footed ferret reintroduction sites in plague free areas will greatly assist in managing the impacts of the disease on black-footed ferret reintroduction.

Another promising prospect is presented by the results of surveys of white-tailed prairie dogs and black-footed ferrets in Shirley Basin, Wyoming. The data indicate that this area, and perhaps others in the white-tailed prairie dog range, may have proportionately higher value than previously thought because both prairie dogs and black-footed ferrets have maintained significant populations in the presence of plague since monitoring was begun in 1991 (Luce 2002; Grenier et al. 2004, Grenier 2008). In fact, both white-tailed prairie dog and black-footed ferret numbers increased over 10 years despite at least one plague epizootic (Grenier et al. 2004, Grenier 2008).

However, black-tailed prairie dog data presented by Cully and Williams (2001) suggest that a fundamental change may be occurring in prairie dog ecology whereby some large colonies and/or complexes may not persist when repeatedly challenged by plague. Persistence of only small colonies or complexes may have serious implications for black-footed ferret recovery. Few large sites may persist at their full habitat capability in the face of repeated plague epizootics. Therefore, establishing and maintaining a large number of sites over the range of the species probably represent the most effective way to meet Recovery Plan goals.

Since black-footed ferret recovery and prairie dog management issues are closely tied, the future of the black-footed ferret essentially depends on developing effective management of black-tailed, white-tailed, and Gunnison's prairie dogs. The Western Association of Fish and Wildlife Agencies' Prairie Dog Conservation Team developed the Black-tailed Prairie Dog Conservation Assessment and Strategy (Van Pelt 1999) and the Black-tailed Prairie Dog Multi-state Conservation Plan (Luce 2003), a guideline for development of state black-tailed prairie dog management plans. Black-tailed prairie dog management plans have been completed in Arizona, Colorado, Kansas, Montana, New Mexico, North Dakota, Oklahoma, South Dakota, Texas and Wyoming. The Arizona Game and Fish Department is currently reintroducing black-tailed prairie dogs in southeastern Arizona.

The Black-tailed Prairie Dog Multi-state Conservation Plan includes several provisions that complement those of the Black-footed Ferret Recovery Plan and many state black-tailed prairie dog conservation plans identify significant complexes, allowing for management of these areas to occur on many fronts.

Management strategies for black-tailed prairie dogs on tribal lands were first prepared for the Intertribal Prairie Ecosystem Restoration Consortium in January 2002 (Vosburgh pers comm. 2003). The goal for each tribe was to develop and implement management programs for the conservation of prairie dog habitat. The Lower Brule and Ft. Belknap Reservations have final prairie dog management plans in place, and draft plans have been prepared for the Ft. Berthoud, Northern Cheyenne, Crow Creek, and Rosebud Reservations.

The states of Wyoming, Colorado, Utah, and Montana developed a Conservation Assessment for the white-tailed prairie dog in 2004 (Seglund et al. 2004) and the states of Arizona, New Mexico, Colorado, and Utah completed Conservation Assessment for the Gunnison's prairie dog in 2007 (Western Association of Fish and Wildlife Agencies 2007). As part of the Conservation Assessments, white-tailed and Gunnison's prairie dog complexes were identified, allowing for preparation of site-specific management plans in the near future.

SUMMARY

The black-footed ferret recovery program has faced and overcome several obstacles. Foremost were capture of the wild population at Meeteetse, captive breeding, development of release strategies, and release site identification based on habitat suitability, agency and private landowner cooperation, and other factors. Given that those obstacles to success were overcome, continued progress on black-footed ferret recovery now depends upon identification and active management of additional reintroduction sites. I identify 181 sites that might meet the biological and habitat suitability requirements for reintroduction of black-footed ferrets within 3-10 years. Site development is contingent upon directed management emphasis, state and federal agency management priority, and, if on private land, private landowner concurrence based on agreements or incentives.

The members of the Black-footed Ferret Recovery Implementation Team and Prairie Dog Conservation Teams are encouraged to evaluate the sites presented in this paper and develop strategies to begin management of as many sites as possible for black-footed ferret reintroduction within 10 years.

Key Components for Success:

- Involvement of private landowners will be critical to black-footed ferret recovery. Approximately 87% of the area currently inhabited by black-tailed prairie dogs is privately owned (Luce et al. 2006). Despite oft-repeated generalizations research has found that many ranchers, 18% in a 2001 Wyoming study, agree that conservation of prairie dogs is important (Wyoming Agricultural Statistics Service 2001). State Game and Fish agencies must take the lead in initiating programs to manage prairie dogs in cooperation with willing landowners. Good relationships must be created and fostered.

- Development of a landowner incentive program which encourages participation of private landowners in grassland species conservation, including prairie dogs and black-footed ferrets, is another critical component of black-footed ferret recovery. A coalition of groups including the Western Association of Fish and Wildlife Agencies, U.S. Fish and Wildlife Service, National Wildlife Federation, Wildlife Management Institute, Predator Conservation Alliance, and Environmental Defense collectively worked for several years to develop a landowner incentive program for grassland conservation (Luce et al. 2006). Ultimately, the High Plains Partnership was funded in 2004 and uses funds from the Farm Bill to finance grassland conservation incentive programs. Under a new Presidential administration in 2009 the opportunity may exist to significantly expand federal landowner incentive programs through State Wildlife Grants, the Farm Bill, or other avenues. When federal and state agencies identify potential recovery sites in areas that are predominantly private land, the first step in site development should include using available programs to gain private landowner support.

- The U.S. Fish and Wildlife Service effectively used the non-essential, experimental population designation set forth in Section 10(j) of the Endangered Species Act of 1973 to accomplish reintroduction at most sites. These populations do not retain endangered status, but are protected from purposeful ‘take.’ Expanding Section 10(j) to cover an entire state rather than just individual sites would allow the lead on-the-ground agency maximum latitude in developing sites and if necessary translocating black-footed ferrets between sites on short notice. I recommend the U.S. Fish and Wildlife Service continue to pursue this approach. Despite the fact that some ferrets have been released under provisions of experimental research permits ((Section 10(a)(1)(A)) in which reintroduced ferrets remain endangered, but similar protections and assurances (as 10j) are extended to adjacent private land owners, Section 10(j) is likely to remain the most viable option for reintroduction since it is the most palatable to private landowners and federal grazing lessees.

- As suggested in the Recovery Plan, consider all active reintroduction sites as transient since weather events, plague, and other factors can reduce an individual site to little or no value within less than a year. As demonstrated at UL Bend National Wildlife Refuge (R. Matchett pers comm. 2008) and Shirley Basin, Wyoming (Grenier 2008), research to document the impacts of weather, disease, etc. on impacted populations of prairie dogs and black-footed ferrets can provide valuable data for future management. Therefore, immediate translocation is not necessarily the first or only option. However I recommend a plan be in place for each site that lists the thresholds at which black-footed ferrets could be captured and translocated, where they would be taken, and how many would go to each transplant location if that option were exercised.

- Entities within the same jurisdiction such as Wind Cave, Badlands, and Theodore Roosevelt the National Parks should consider the individual parks as components of a mega-reintroduction site. National Grasslands, including Thunder Basin, Little Missouri, Cimarron, Kiowa, Comanche, Pawnee, and others could function similarly within the U.S. Forest Service. This approach would facilitate interchange of management approaches and translocation of black-footed ferrets between sites.

- From the standpoint of the public good, National Grasslands should be managed for maximum wildlife conservation benefits including prairie dogs and black-footed ferrets. Over 75% of the land area within national grasslands is probably suitable for occupation by prairie dogs, but less than 2% is occupied (U.S. Fish and Wildlife Service 2001). A recent proposed amendment to land and resource management plans for three National Grasslands would institute a 3% cap on the amount of prairie dog occupied area on any individual National Grassland. No decisions have yet been made regarding the proposed amendment, but one of the alternatives proposed eliminating over 90% of the area currently occupied by black-footed ferret at Conata Basin. While the proposed amendment evaluated 5 alternatives and offered no preferred alternative, it appears the Forest Service is moving towards capping prairie dog occupied area on these Grasslands at levels far below historical occupancy.

  The 3% cap on prairie dog occupied area along with broader discretion for toxicant use on remaining prairie dogs would compromise the ability of these Grassland Units to contribute towards meaningful black-footed ferret conservation. If other Federal Agencies enacted similar restraints on prairie dog acreage it would likely push most of the black-footed ferret recovery efforts onto non federal lands. Such an approach is contrary to the Endangered Species Act (section 7(a)(1) which requires federal agencies to utilize their authorities in furtherance of the Act by carrying out programs for the conservation of listed species (Larson pers comm. 2008). To do otherwise is unconscionable. The 3% cap will severely limit the number of areas on National Grasslands that can function as black-footed ferret reintroduction sites. Several black-tailed prairie dog complexes of > 2,025 ha will be needed over the range of the species to meet black-footed ferret recovery plan objectives for downlisting and the National Grasslands should be expected to provide several of those sites (Proctor et al. 2006).

- This paper lists 181 potential reintroduction sites but does not prioritize them within an individual state. Prioritization will be the responsibility of the respective organizations implementing development and management. With several biologically suitable sites to choose from in each state, many with private landowner acceptance concerns, prioritization may be an overwhelming task if approached at a statewide level. Therefore I suggest evaluation begin by choosing 5-10 sites and conducting a preliminary evaluation at each. If no significant pitfalls to success are found, a site could advance through successive evaluations until final acceptance. If an individual site fails at any level of evaluation, another site can be added to keep the number of sites being intensively evaluated at 5-10.

- Identification of sites on private or mixed public/private lands as I have done in the paper is a very preliminary first step. On-the-ground contact with landowners is the next step and must be approached at a one-on-one level between landowners and local agency personnel.

- I do not list the sites in a given state from largest prairie dog complex to smallest because I do not believe that the largest sites necessarily have the best potential for development and/or long term viability. It is important not to get hung up trying to develop one particular site because it is the “best” while ignoring other possible sites.

- Ranches owned by out of state landowners, or local conservation-minded landowners who have not been approached to date, may be open to the idea of black-footed ferret reintroduction. This avenue should be enthusiastically pursued at a local level.

- Small, isolated complexes may be the best starting point in private land areas for several reasons. The number of private landowners involved is likely to be smaller, mapping will be easier, the black-footed ferret population will be better confined, and the survey area will be small and confined.

- When starting reintroductions in new areas such as Oklahoma, Nebraska, North Dakota, or Texas consider evaluating several sites at one time rather than focus too much pressure on a single site. Consider a “Demonstration Site” approach to illustrate how state-sponsored landowner incentives and cooperative management can reduce the impact on private lands

- Ten years is a long time in the realm of planning. Ranch managers, land ownership, land use, landowner principles, and federal priorities may change significantly. Prairie dog control will become progressively more expensive and marginal making even small landowner incentives more and more attractive.

LIST OF PERSONAL COMMUNICATIONS

Albee, M. Bureau of Land Management (retired), Colorado
Beierman, H. Muleshoe National Wildlife Refuge, Texas
Byer, T. Thunder Basin National Grassland, Wyoming
Canestorp, M. U.S. Fish and Wildlife Service, Pueblo Army Depot, Colorado
Clawges, R. Ft. Carson Military Reservation, Colorado
Conway, C. University of Arizona
Danvir, R. Deseret Land and Cattle Company, Utah
Fargey, P. Grasslands National Park, Canada
Fritz, M. Nebraska Game and Parks Commission
Garcia, D. U. S. Forest Service, New Mexico
Grenier, M. Wyoming Game and Fish Department
Hanebury, L. U. S. Fish and Wildlife Service, Montana
Hastings, B. Rocky Mountain Arsenal, Colorado
Hoagland, J. Oklahoma Department of Wildlife Conservation
Humphrey, B. Pawnee National Grassland, Colorado
Klavetter, M. U.S. Army Pinyon Canyon Maneuvers Site, Colorado
Larson, S. U. S. Fish and Wildlife Service, South Dakota
List, R. Instituto de Ecologia, Mexico
Lockhart, M. U.S. Fish and Wildlife Service (retired)
Long, D. Turner Endangered Species Foundation, New Mexico
Luce, R. Wyoming Game and Fish Department (retired)
Manes, R. The Nature Conservancy, Kansas
Matchett, R. UL Bend National Wildlife Refuge, Montana
Mikesic, D. Navaho Nation, Arizona
Morrison, P. U. S. Forest Service, New Mexico (retired)
Mulhern, D. U.S. Fish and Wildlife Service, Kansas
Orabona-Cervoski, A. Wyoming Game and Fish Department
Oehler, D. Theodore Roosevelt National Park, North Dakota
Shively, S. Comanche National Grassland, Colorado
Singhurst, J. Texas Parks and Wildlife Department
Svingen, D. Little Missouri National Grassland, North Dakota
Truett, J. Turner Endangered Species Foundation, New Mexico
Van Pelt, B. Arizona Game and Fish Department
Vosburgh, T. Intertribal Prairie Ecosystem Restoration Consortium
Wagner, D. Northern Arizona University

Weimers, L. Oklahoma Department of Wildlife Conservation
Young, J. Texas Parks and Wildlife Department

LITERATURE CITED

Antolin, M.F., P. Gober, B. Luce, D.E. Biggins, W.E. Van Pelt, D.B. Seery, M. Lockhart, and M. Ball. 2002. The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. Transactions of the 67th North American Wildlife and Natural Resources Conference. Wildlife Management Institute, Washington, D.C.

Arizona Game and Fish Department and Navaho Natural Heritage Program. 1996. Survey and evaluation of Gunnison's prairie dog. Arizona Game and Fish Department Heritage Grant I93084. 19pp.

Biggins, D.C., B.J. Miller, L.R. Hanebury, B. Oakleaf, A.H. Farmer, R. Crete and A. Dood. 1993. A technique for evaluating black-footed ferret habitat in Management of prairie dog complexes for reintroduction of the black-footed ferret, U.S. Fish and Wildlife Service, Biological Report 13. 97 pp.

Biggins, D. 2003. Decline of a white-tailed prairie dog population near Meeteetse, Wyoming. U.S. Geological Survey – Biological Resources Division. Prairie Dog Research Update #8, 5 November 2003.

Bischof, R., M.J. Fritz, and M.A. Hack. 2004. Aerial survey of black-tailed prairie dogs (*Cynomys ludovicianus*) in Nebraska. Nebraska Game and Parks Commission, Wildlife Division, Lincoln. 10pp.

Black-footed Ferret Advisory Team. 1990. A cooperative management plan for black-footed ferrets at Meeteetse. Wyoming Game and Fish Department, Cheyenne, WY. 45pp.

Boschen, N.S. 1986. Black-footed ferret study in the Cisco Desert area of Utah introductory report. Utah Division of Wildlife Resources, Salt Lake City, Utah.

Cain, S.A., J.A. Kadlec, D.L. Allen, R.A. Cooley, M.G. Hornocker, A.S. Leopold, and F.H. Wagner. 1972. Predator control – 1971. Report to the Council on Environmental Quality and the Department of the Interior by the Advisory Committee, University of Michigan. Ann Arbor. 207 pp.

Clark, T.W. and T.M. Campbell III. 1981. Additional black-footed ferret (*Mustela nigripes*) reports from Wyoming. Great Basin Naturalist 41: 360-361.

Colorado Division of Wildlife. 2003a. Conservation plan for grassland species in Colorado. Denver. 38 pp.

Colorado Division of Wildlife. 2003b. Report of acreages of active colonies for Gunnison's and white-tailed prairie dogs in Seglund, A.E., A.E. Ernst, M. Grenier, B. Luce, A. Puchniak and P. Schnurr. 2004. White-tailed Prairie Dog Conservation Assessment. Prairie Dog Conservation Team, Price, UT. 152pp.

Conway, C.J. 1989. Evaluation of potential black-footed ferret reintroduction sites in Wyoming. Report prepared for the Wyoming Game and Fish Department. 10 pp.

Cranney, S.J. and K.S. Day. 1994. 1993 prairie dog density surveys in the Diamond Mountain Resource Area. Utah Division of Wildlife, Northeast Region, Vernal. 8 pp.

Cully, J.F., Jr. 1993. Plague in prairie dog ecosystems: importance for black-footed ferret management. In the prairie dog ecosystem, managing for biological diversity. Montana BLM Wild. Tech. Bull. No. 2. Pp. 47-55.

Cully, J.F. and E.S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82: 894-905.

Cully, J.F., D.E. Biggins, and D.B. Seery. 2006. Conservation of prairie dogs in areas with plague. Pages 157-168 in Conservation of the black-tailed prairie dog. J.L. Hoogland, Editor, Island Press. 350pp.

EDAW, Inc. 2000. Black-tailed prairie dog study of eastern Colorado. Report to the Colorado Department of Natural Resources, Denver.

Ernst, A.E. 2001. Changes in black-tailed prairie dog towns on the Texas panhandle determined by a geographic information system. M.S. Thesis. Texas Tech University, Lubbock. 99 pages.

Grenier, M., A. Carpenter, M. Martin, M. Purcell, and J. Stephens. 2003. Black-footed ferret habitat evaluation of historical white-tailed prairie dog complexes in Wyoming - completion report, April 2003. Wyoming Game and Fish Department, Lander. 19pp.

Grenier, M. 2004. An evaluation of black-footed ferret block clearance in Wyoming. Pages 5-18 in Threatened, Endangered, and Nongame Bird and Mammal Investigations Annual Completion Report, Nongame Section, Wyoming Game and Fish Department, Lander, November 2004

Grenier, M., B. Oakleaf, K. Taylor, and M. Hymas. 2004. Inventory and mapping of black-tailed prairie dogs in Wyoming - an estimate of acreage. Pages 114-133 in Threatened, Endangered, and Nongame Bird and Mammal Investigations Annual Completion Report, Nongame Section, Wyoming Game and Fish Department, Lander, November 2004.

Grenier, M.B. 2008. Population biology of the black-footed ferret reintroduced into Shirley Basin, Wyoming. M.S. Depeartment of Zoology and Physiology, University of Wyoming, Laramie. 90pp.

Hansen, R.M. 1988. Chronology of prairie dog control operations and related developments in South Dakota. Pages 121-122 *in* Eighth Great Plains Animal Damage Control Workshop, Rapid City, South Dakota. USDA Forest Service General Tech. Rept. RM-154, D.W. Uresk, G.L. Schenbeck, and R. Cefkin, eds.

Hnilicka, P. and B. Luce. 1992. Habitat evaluation of the Shirley Basin/Medicine Bow black-footed ferret management area and selection of criterion for the premier reintroduction site in Oakleaf, B., B. Luce, E.T.Thorne, and S. Torbit in 1991 Annual Completion Report – Black-footed Ferret Reintroduction Shirley Basin, Wyoming. Wyoming Game and Fish Department, Lander. 240 pp.

Johnson, K., T. Neville, and L. Price. 2003. Remote sensing survey of black-tailed prairie dog towns in the historical New Mexico range. New Mexico Natural Heritage Program, University of New Mexico, Albuquerque. 28 pp.

Kansas Black-tailed Prairie Dog Working Group. 2002. Kansas black-tailed prairie dog conservation and management plan. Pratt. 29 pp.

Kempema, S. L. F. 2007. South Dakota black-tailed prairie dog colony acreage and distribution, 2006. South Dakota Department of Game, Fish, and Parks, Wildlife Division Report Number 2007-07, Pierre. 21pp.

Knowles, C.J. 2003. Status of the black-tailed prairie dog in North Dakota. Report prepared for the North Dakota Game and Fish Department, Bismarck. 56 pp.

Knowles, C.J. 2007. Status of the black-tailed prairie dog in North Dakota. Report prepared for the North Dakota Game and Fish Department, Bismark. 14pp.

Lockhart, J. M. 1998-2007. U.S. Fish & Wildlife Service. Annual Letter to Black-footed Ferret Recovery Implementation Team. In litt.

Lomolino, M.V. and G.A. Smith. 2001. Dynamic biogeography of prairie dog (*Cynomys ludovicianus*) towns near the edge of their range. Journal of Mammalogy 82(4):937-945.

Lomolino, M. V., G.M. Smith, and V. Vidal. 2002. Long-term persistence of prairie dog towns: insights for designing networks of prairie reserves. Biological Conservation 115: (2002) 111-120.

Luce, R. J. 2002. Black-footed ferret release site monitoring in Shirley Basin, Wyoming. Page 15 in Proceedings of an American Southwest Workshop – Landscape ecology of plague in the American Southwest, September 19-20, 2000, C.J. Brand, Editor, Ft. Collins, CO.

Luce, R. J. 2003. A multi-state conservation plan for the black-tailed prairie dog, *Cynomys* *ludovicianus,* in the United States – an addendum to the Black-tailed Prairie Dog Conservation Assessment and Strategy, November 3, 1999. Prairie Dog Conservation Team, Sierra Vista, AZ. 79pp.

Luce, R.J. 2005a. Areas where habitat characteristics could be evaluated to identify potential black-footed ferret reintroduction sites and develop conservation partnerships. Pages 69-88 in Proceedings of the symposium on the status of the black-footed ferret and its habitat, Fort Collins, Colorado, January 28-29, 2004. U.S. Department of the Interior, U.S. Geological Survey Scientific Investigations Report 2005-5293. 288pp.

Luce, R.J. 2005b. Identification of sites occupied by Gunnison's prairie dog before 1984 and determination of current status at those sites in Catron and Socorro counties, New Mexico. New Mexico Department of Game and Fish Share with Wildlife Contract No. 05-516.0000.0017. 19pp.

Luce, R.J., R. Manes, and B. Van Pelt. 2006. A multi-state plan to conserve prairie dogs. Pages 210-217 in Conservation of the black-tailed prairie dog. J.L. Hoogland, Editor, Island Press. 350pp.

Martin, D. and B. Luce. 1990. Black-footed ferret surveys in 1990 Nongame Program Annual Completion Report. Wyoming Game and Fish Department, Lander. 220pp.

Montana Prairie Dog Working Group. 2002. Conservation plan for black-tailed and white-tailed prairie dogs in Montana. Helena. 51pp.

Northern Cheyenne Indian Reservation. 2008. Black-footed ferret allocation request for Northern Cheyenne Indian Reservation. March 14, 2008

Orabona-Cerovski, A. 1991. Habitat characteristics, population dynamics, and behavioral interactions of white-tailed prairie dogs in Shirley Basin, Wyoming. MS Thesis, University of Wyoming, Laramie. 182pp.

Parrish, T.L. and B. Luce. 1990. Evaluation of potential black-footed ferret reintroduction sites in Wyoming. Wyoming Cooperative Fish and Wildlife Research Unit and Wyoming Game and Fish Department, Laramie.

Proctor, J. B. Haskins, and S.C. Forrest. 2006. Focal areas for conservation of prairie dogs and the grassland ecosystem. Pages 232-247 in Conservation of the black-tailed prairie dog. J.L. Hoogland, Editor, Island Press. 350pp.

Seglund, A.E., A.E. Ernst, M. Grenier, B. Luce, A. Puchniak and P. Schnurr. 2004. White-tailed Prairie Dog Conservation Assessment. Prairie Dog Conservation Team, Price, UT. 152pp.

Steinauer, E.M. and S.L. Collins. 1996. Prairie Ecology – the tallgrass prairie in Prairie

Conservation, F.B. Sampson and F.L. Knopf, eds. Island Press, Washington, D.C. and Covelo, CA. 340pp.

Svingen, D. 2004. Black-tailed prairie dog conservation assessment and strategy: Grand River Ranger District. Dakota Prairie Grasslands, internal report. September 30, 2004. 97pp. + appendices.

Svingen, D. 2006a. Black-tailed prairie dog conservation assessment and strategy: Medora Ranger District. Dakota Prairie Grasslands, internal report. May 5, 2006. 82pp.

Svingen, D. 2006b. Black-tailed prairie dog conservation assessment and strategy: McKenzie Ranger District. Dakota Prairie Grasslands, internal report. December 8, 2006. 79pp.

U.S. Fish and Wildlife Service. 1988. Black-footed ferret recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado. 154 pp.

U.S. Fish and Wildlife Service. 2000. 12-month finding for a petition to list the black-tailed prairie dog as threatened. Federal Register 65:5476-5488), February 4, 2000.

U.S. Fish and Wildlife Service. 2001. Candidate and listing priority assignment form. Summarized in Federal Register 66(210):54808-54832. February 20, 2001.

Van Pelt, W.E. 1999. The black-tailed prairie dog conservation assessment and strategy. Arizona Game and Fish Department, Phoenix. 55pp.

Wagner, D.M. and C. Drickamer. 2002. Distribution, habitat use, and plague in Gunnison's prairie dogs in Arizona. Heritage Grant I20009. Report to the Arizona Game and Fish Department. 50 pp.

Wagner, D.M., L.C. Drickamer, D. M. Krpata, C.J. Allender, W.E. Van Pelt, and P. Klein. 2006. Persistence of Gunnison's prairie dog colonies in Arizona, USA. Biological Conservation 130: 331-339.

Western Association of Fish and Wildlife Agencies. 2007. Gunnison's prairie dog conservation assessment: addendum to the white-tailed and Gunnison's prairie dog conservation strategy. Western Association of Fish and Wildlife Agencies. Laramie, Wyoming.

Wyoming Agricultural Statistics Service. 2001. Black-tailed prairie dog management survey: report of results to Wyoming Game and Fish Department. Wyoming Department of Agriculture, Cheyenne, Wyoming.

Young, P.J. 2008. Screening for plague resistance in black-tailed prairie dogs on U.S. Army Pueblo Chemical Depot. Prairie Ecosystems Research Group. 17pp.

Table 1. Active and Immediate Potential Black-footed Ferret Reintroduction Sites in 2008.

State	Site Name	Nearest Town	Plague Status*
		Active	
Arizona	Aubrey Valley	Seligman	Not Present
	Espee Ranch	Seligman	Not Present
Colorado	Wolf Creek	Dinosaur	Present
Kansas	Smoky Valley Ranch	Oakley	Not Present
Montana	UL Bend NWR	Malta	Present
	Ft. Belknap Reservation	Malta	Present
	BLM 40-Complex	Malta	Present
	N. Cheyenne Reservation	Miles City	Present
New Mexico	Vermejo Park Ranch	Raton	Not Present
South Dakota	Cheyenne R. Reservation	Pierre	Present
	Badlands National Park	Wall	Not Present
	Conata Basin/Badlands NP	Wall	Present
	Rosebud Reservation	Mission	Not Present
	Lower Brule Reservation	Pierre	Not Present
	Wind Cave National Park	Hot Springs	Not Present
Utah	Coyote Basin	Dinosaur	Present
Wyoming	Shirley Basin	Medicine Bow	Present
Chihuahua	Janos	Janos	Not Present
		Immediate Potential	
Canada	Grasslands NP	Swift Current	Not Present
Colorado	Ft. Carson	Colorado Springs	Present
Wyoming	Saratoga	Saratoga	Present

* Plague Status

Present: plague has been documented at the site or in the vicinity at some time
Not Present: field surveys have not documented plague at the site or in the vicinity; or the site lies east of the plague line
Unknown: plague status unknown due to lack of data (plague probably occurs at or in the vicinity of sites west of the plague line)

Table 2. Intermediate Potential Black-footed Ferret Reintroduction Sites in 2008.

State	Site Name	Nearest Town	Plague Status*
Arizona	Canyon Diablo	Winslow	Present
	Coconino Plateau East	Seligman	Not Present
	Coconino Plateau Navaho	Seligman	Not Present
	East of Flagstaff	Flagstaff	Present
	East of Seligman	Seligman	Present
	Elephant Butte	Dilkon	Present
	Leupp	Winslow	Present
	Red Lake	Winslow	Present
	West of Dilkon	Dilkon	Present
	West of Wupatki NM	Flagstaff	Present
Colorado	Baca County (2 complexes)	Springfield	Present
	Bent County (3 complexes)	Lamar	Present
	Crowley County (1 complex)	Rocky Ford	Present
	Kit Carson County (1 complex)	Burlington	Present
	Prowers County (3 complexes)	Lamar	Present
	Pueblo County (2 complexes)	Pueblo	Present
	Weld County (5 complexes)	Greeley	Present
	Cimarron NG	Springfield	Present
	Comanche NG - Carizzo	Pritchett	Present
	Comanche NG - Timpas	La Junta	Present
	Pawnee NG	Greeley	Present
	Pinyon Canyon Maneuvers Site	La Junta	Present
	Pueblo Army Depot	Pueblo	Present
	Rocky Mountain Arsenal	Denver	Present
	BLM Twin Lakes	Alamosa	Present
	Parlin	Gunnison	Present
	Northwest Moffat County	Craig	Present
Kansas	Cheyenne County (4 complexes)	Wheeler	Not Present
	Ford County	Dodge City	Not Present
	Greeley County	Horace	Not Present
	Hamilton County	Syracuse	Not Present
	Hodgeman County	Gray	Not Present
	N. Kearney County	Garden City	Not Present
	S. Kearney County	Garden City	Not Present
	Kiowa, Comanche, Clark Counties	Coldwater	Not Present
	Logan, Sherman County	Oakley	Not Present
	Rawlins County	Atwood	Not Present

	Scott County	Modoc	Not Present
	Stevens County (3 complexes)	Moscow	Not Present
	Thomas County	Colby	Not Present
	Z-Bar Ranch	Medicine Lodge	Not Present
Montana	Big Sandy	Havre	Present
	Custer Creek	Miles City	Present
	Fergus and Petroleum Counties	Lewistown	Present
	Ingomar	Miles City	Present
	Leachman, Crow Reservation	Billings	Present
	Lower Tongue River	Mile City	Present
	Upper Musselshell	Lewistown	Present
	Upper Tongue River	Miles City	Present
	Valley County	Glasgow	Present
Nebraska	Box Butte	Alliance	Not Present
	Buffalo County	Kearney	Not Present
	Chase County	Imperial	Not Present
	Cheyenne County	Sydney	Not Present
	Custer County	Broken Bow	Not Present
	Dawes County	Chadron	Not Present
	Dawson County	Lexington	Not Present
	Deuel County	Chappell	Not Present
	Dundy County	Benkelman	Not Present
	Frontier County	Curtis	Not Present
	Furnas County	Arapahoe	Not Present
	Greeley County	Greeley	Not Present
	Harlan County	Alma	Not Present
	Hayes County	Hayes Center	Not Present
	Hitchcock County	Trenton	Not Present
	Keith County	Ogallala	Not Present
	Lincoln County	North Platte	Not Present
	Morrill County	Bayard	Not Present
	Perkins County	Grant	Not Present
	Red Willow County	McCook	Not Present
	Sherman County	Loup City	Not Present
	Scotts Bluff County	Scottsbluff	Not Present
	Sioux County	Harrison	Not Present
	Blue Creek Ranch	Oshkosh	Not Present
	Oglala National Grassland	Chadron	Not Present
New Mexico	Chavez Ranch	Quemado	Unknown
	Frenches Draw	Quemado	Unknown
	Johnson Basin	Quemado	Unknown

	Lea County	Lovington	Unknown
	Quay/Curry Counties	Tucumcari	Unknown
	Roosevelt County	Portales	Unknown
	Union County	Clayton	Unknown
North Dakota	NW McKensie Complex		
	Little Missouri NG	Williston	Unknown
	SW McKensie Complex		
	Little Missouri NG	Williston	Unknown
	NE Slope County		
	Little Missouri NG	Dickinson	Unknown
	SW Slope County		
	Little Missouri NG	Marmath	Unknown
	Standing Rock Reservation	North Lemmon	Unknown
	S. Unit Theodore Roosevelt NP	Dickinson	Not Present
	Little Missouri River Complex	Bowman	Not Present
Oklahoma	Beaver County: EC	Beaver	Not Present
	Beaver County: SC	Beaver	Not Present
	Cimarron County: SW	Boise City	Not Present
	Texas County: NC	Guymon	Not Present
	Texas County: EC	Guymon	Not Present
South Dakota	Corson County	Mobridge	Not Present
	Custer County	Custer	Not Present
	Dewey County (off Reservation)	Eagle Butte	Not Present
	Fall River County	Hot Springs	Not Present
	Jackson County	Rapid City	Not Present
	Ziebach County (off Reservation)	Eagle Butte	Not Present
	Bad River Ranch	Pierre	Not Present
	Ft Pierre NG	Pierre	Not Present
	Grand River NG	Mobridge	Not Present
	Pine Ridge Reservation	Pine Ridge	Not Present
	Smithwick Area, Buffalo Gap NG	Hot Springs	Not Present
	Standing Rock Reservation	Lemmon	Not Present
	Triple 7 Ranch	Hermosa	Not Present
Texas	Bailey County + 4 Counties	Morton	Unknown
	Brewster County	Alpine	Unknown
	Cochran County + 3 Counties	Lubbock	Unknown
	Dallam County + 8 Counties	Dalhart	Unknown
	Deaf Smith County + 7 Counties	Amarillo	Unknown
	Floyd County + 3 Counties	Plainview	Unknown
	Hale County	Plainview	Unknown

	Hemphill County + 2 Counties	Canadian	Unknown
	Hockley County + 3 Counties	Lubbock	Unknown
	Hudspeth County	El Paso	Unknown
	Hutchinson County + 3 Counties	Borger	Unknown
	Lipscomb County	Perryton	Unknown
	Lipscomb County + 3 Counties	Perryton	Unknown
	Lynn County	Lubbock	Unknown
	Lynn County + 2 Counties	Lubbock	Unknown
	Midland County + 2 Counties	Odessa	Unknown
	Pecos County + 3 Counties	Ft Stockton	Unknown
	Upton County + 2 Counties	Odessa	Unknown
	Yoakum and Gaines Counties	Brownfield	Unknown
	Muleshoe NWF	Lubbock	Present
	Rita Blanca NG	Dalhart	Unknown
Utah	Buckhorn	Price	Present
	Cisco	Green River	Present
	Crescent Junction	Price	Present
	Eight Mile Flat	Green River	Present
	Huntington	Green River	Present
	Kennedy Wash	Green River	Present
	Rich County	Rich	Unknown
	Shiner Basin	Green River	Present
	Snake John	Green River	Present
	Sunshine Bench	Green River	Present
	Twelve Mile Flat	Green River	Present
	Woodside		
Wyoming	Bolton Ranch	Saratoga	Present
	Carter	Kemmerer	Present
	Cumberland	Kemmerer	Present
	Fifteen-mile	Worland	Present
	Flaming Gorge	Green River	Present
	Kinney Rim	Rawlins	Present
	Meeteetse	Meeteetse	Present
	Moxa	Kemmerer	Present
	Pathfinder	Casper	Present
	Seminoe	Casper	Present
	Shamrock Hills	Rawlins	Present
	Sweetwater	Lander	Present
	Arvada	Gillette	Present
	Bill East	Douglas	Unknown
	Casper North	Casper	Unknown
	Casper South	Casper	Unknown

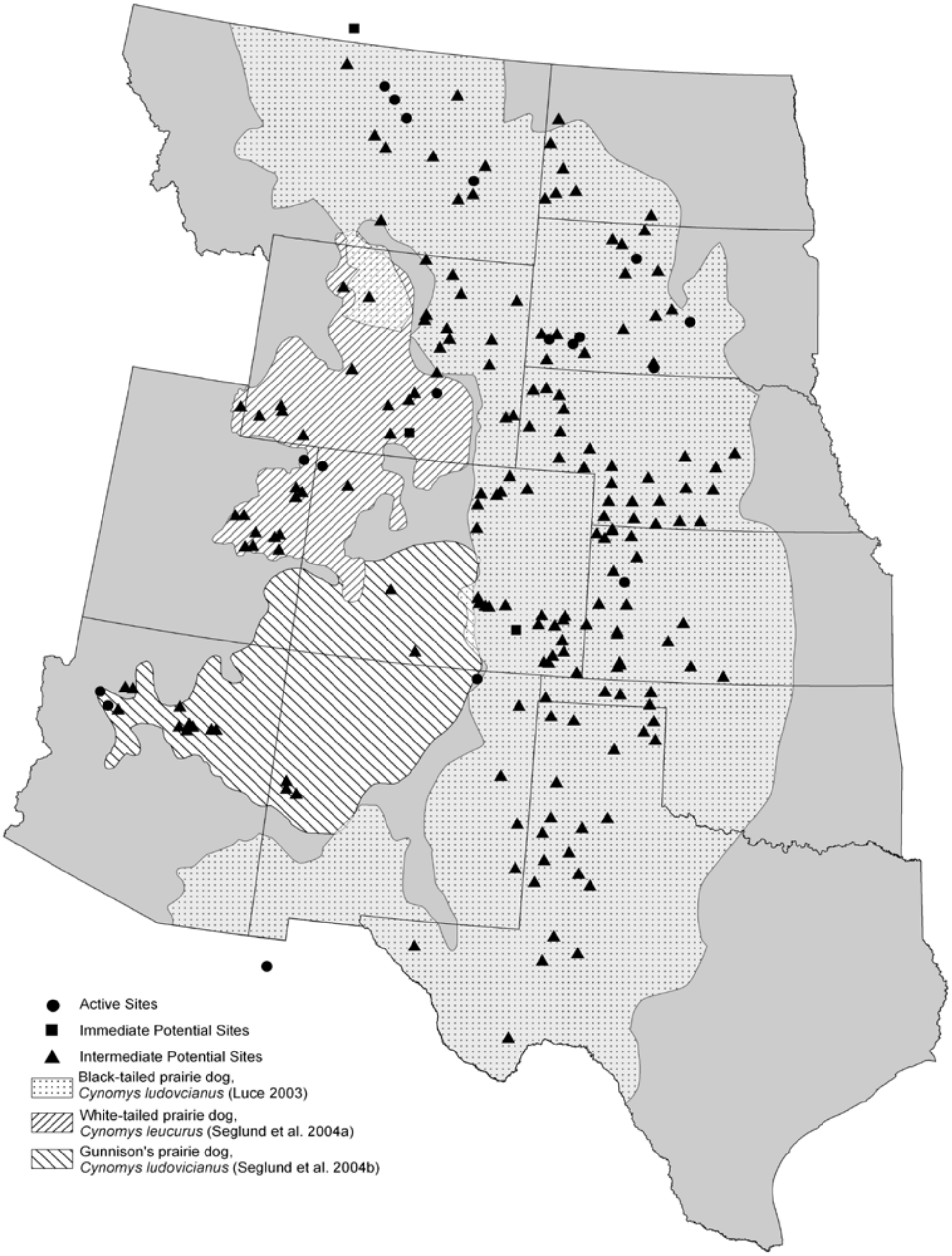
Four Corners	Kaycee	Unknown
Kaycee	Kaycee	Unknown
Linch	Kaycee	Unknown
Moorcroft	Moorcroft	Unknown
Pleasantdale	Gillette	Unknown
Ross	Edgerton	Unknown
Slater	Wheatland	Unknown
Torrington	Torrington	Unknown
Sheridan	Sheridan	Unknown
Thunder Basin National Grassland	Douglas	Present

TOTAL SITES: 181

* Plague Status

Present: plague has been documented at the site or in the vicinity at some time
Not Present: field surveys have not documented plague at the site or in the vicinity; or the site lies east of the plague line
Unknown: plague status unknown due to lack of data (plague probably occurs at or in the vicinity of sites west of the plague line)

Figure 1. Locations of Active, Immediate Potential, and Intermediate Potential black-footed ferret reintroduction sites in 2008.



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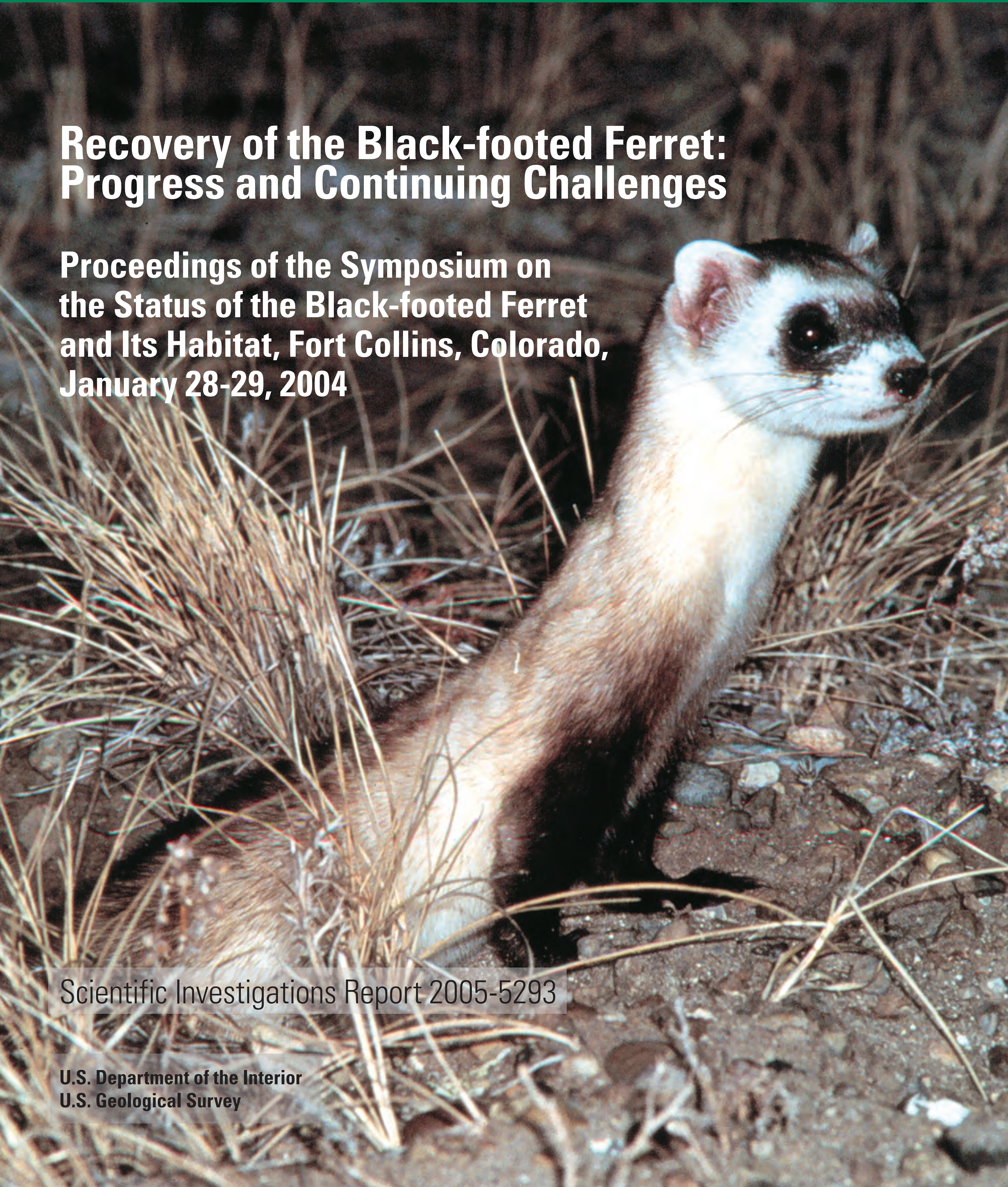

Recovery of the Black-footed Ferret: Progress and Continuing Challenges

Proceedings of the Symposium on the Status of the Black-footed Ferret and Its Habitat, Fort Collins, Colorado, January 28-29, 2004

Scientific Investigations Report 2005-5293

U.S. Department of the Interior
U.S. Geological Survey

Cover photo of black-footed ferret by Dean Biggins taken on
East Core Prairie Dog Colony, Meeteetse, Wyo., February 1983


Heather Branick
1999

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Edited by James E. Roelle, Brian J. Miller, Jerry L. Godbey, and Dean E. Biggins

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Contents

Acknowledgments

The Symposium on the Status of the Black-footed Ferret and Its Habitat, held January 28–29, 2004, in Fort Collins, Colo., and the resulting proceedings contained herein would not have been possible without the dedicated efforts of numerous individuals and agencies. Financial support for the meeting itself and for publication of this volume was provided by Aaron and Gretchen Clark of the Black-footed Ferret Recovery Foundation, by the U.S. Fish and Wildlife Service, and by the U.S. Geological Survey. Sandi Godbey, ably assisted by Jenny Benson, Matt Dunfee, Darren Long, Noe Marymor, Adam Phillips, Adrianna Siniawski, and Ashley Skeen, attended to the infinite variety of details that make a meeting run smoothly. We gratefully acknowledge Dr. Andrew Dobson, Princeton University, Department of Ecology and Evolutionary Biology, for the keynote address, as well as the assistance of Della Garelle, Mike Lockhart, Bill Van Pelt, and Chris Brand, who served as session moderators. We thank Mike Lockhart, Paul Marinari, and Julie Kreeger for hosting a field trip to the National Black-footed Ferret Conservation Center, which at the time of the symposium was under construction but is now a fully functioning facility. We are indebted to Dale Crawford, Delia Story, Jennifer Shoemaker, and especially Dora Medellin for their able assistance in preparing the text and graphics for publication and to Heather Branvold, Patricia Mendoza, and Dale Crawford for graciously allowing us to use their artwork. Finally, we wish to thank the many organizations and countless individuals who have contributed to the Black-footed Ferret Recovery Program. While space does not allow us to mention them individually, it is obvious that neither the symposium nor this volume would have been possible without their unflagging efforts on behalf of one of North America’s most engaging creatures.

Dedication

In the period between January 2004, when this symposium took place, and publication of the proceedings presented here, partners in the Black-footed Ferret Recovery Program suffered enormous personal and professional losses through the deaths of Tom Thorne, Beth Williams, Bill Russell, and Stan Anderson.

Tom and Beth, a husband and wife team of professional veterinarians and wildlife biologists, were killed in a traffic accident on their way home to Laramie, Wyo., on December 29, 2004. Both Tom and Beth were responsible for much of the original recovery program leadership and were deeply involved in all elements of black-footed ferret management and research. Their expertise and many notable scientific contributions significantly advanced our knowledge and capabilities related to black-footed ferret captive breeding, disease risks and management, vaccine efficacy and safety, and reintroduction.

Bill Russell died at Ivinson Hospital in Laramie on August 16, 2005. Bill was a Professor of Animal Science at the University of Wyoming for 25 years and was the official Black-footed Ferret Species Survival Plan® studbook keeper and genetic advisor for many years. Bill provided invaluable advice and recommendations on captive black-footed ferret management and breeding.

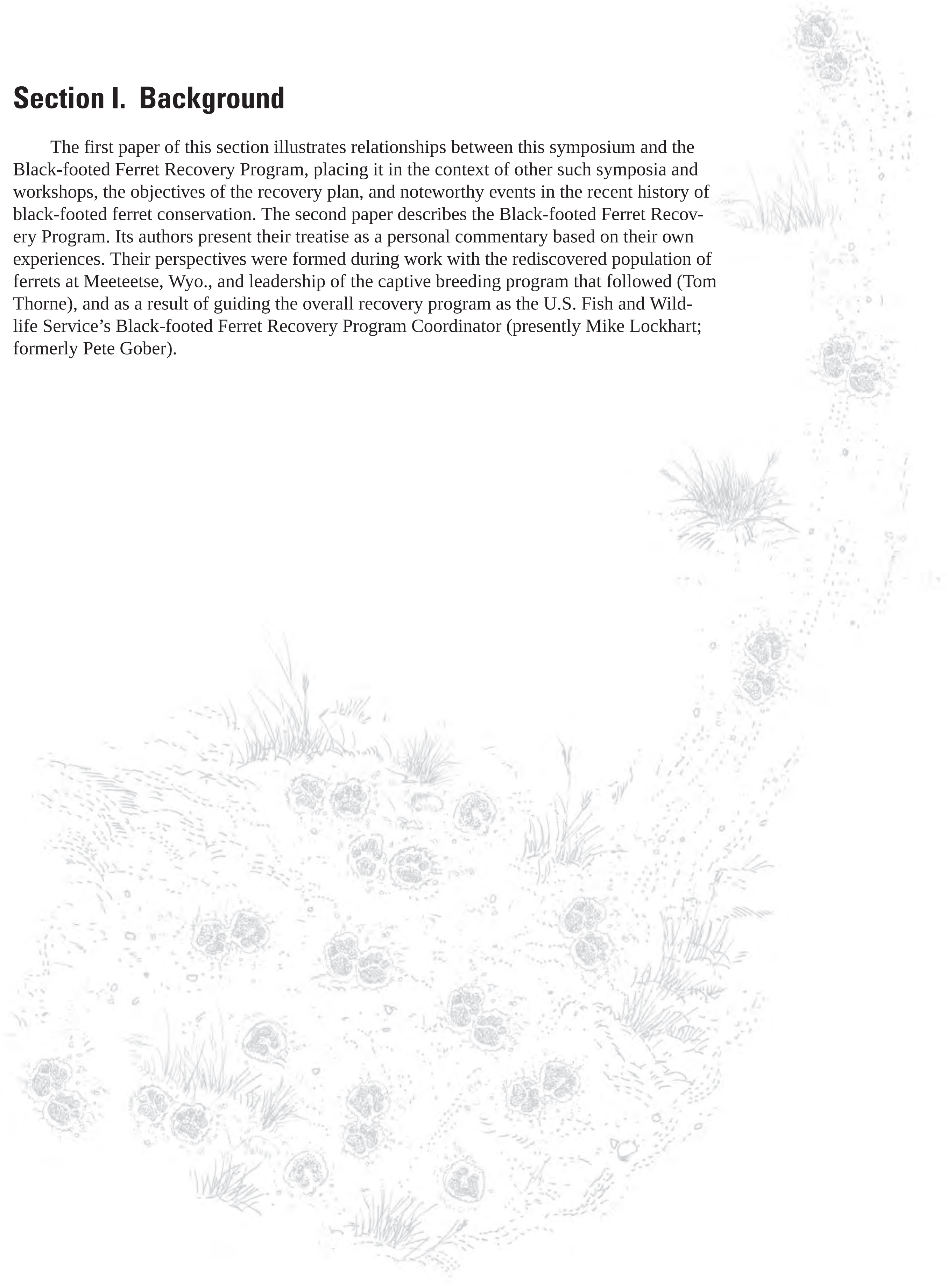
Stan Anderson died at his home in Laramie on September 1, 2005, following an extended illness. Stan started the University of Wyoming Cooperative Fish and Wildlife Research Unit in 1980 and served as a graduate advisor for many biologists who obtained advanced degrees studying various aspects of prairie dog conservation and black-footed ferret recovery.

These proceedings are dedicated to the memory and accomplishments of these long-time ferret recovery advocates, scientists, advisors, administrators, and mentors. The loss of these fine individuals leaves a substantial void in the institutional knowledge and foundation of the Black-footed Ferret Recovery Program and in the wildlife conservation community as a whole. They will be deeply missed, but their legacy will endure.


Heather
'08

Section I. Background

The first paper of this section illustrates relationships between this symposium and the Black-footed Ferret Recovery Program, placing it in the context of other such symposia and workshops, the objectives of the recovery plan, and noteworthy events in the recent history of black-footed ferret conservation. The second paper describes the Black-footed Ferret Recovery Program. Its authors present their treatise as a personal commentary based on their own experiences. Their perspectives were formed during work with the rediscovered population of ferrets at Meeteetse, Wyo., and leadership of the captive breeding program that followed (Tom Thorne), and as a result of guiding the overall recovery program as the U.S. Fish and Wildlife Service's Black-footed Ferret Recovery Program Coordinator (presently Mike Lockhart; formerly Pete Gober).



The Symposium in Context

By Dean E. Biggins[1]

The black-footed ferret (*Mustela nigripes*) is a member of the weasel family (Mustelidae) and is closely related to the Siberian polecat (*M. eversmannii*) of Asian steppes and the European polecat (*M. putorius*). Compared to its relatives, the black-footed ferret is an extreme specialist, depending on the prairie dogs (*Cynomys* spp.) of North American grasslands for food and using prairie dog burrows for shelter. The black-footed ferret's close association with prairie dogs was an important factor in its decline. Prairie dogs were regarded as an agricultural pest as human settlement progressed westward, and they became important hosts for plague as that disease colonized eastward from its sources of introduction on the west coast. Prairie dog numbers were dramatically reduced by poisoning, cropland conversions, and plague during the first half of the 20th century, and black-footed ferret populations declined precipitously. The black-footed ferret was included on the first lists of endangered species, and its status was precarious by the time the Endangered Species Act of 1973 was passed. Its rebound from a low point of 10 known individuals in spring of 1985 (Biggins and others, 2006) is impressive, but the species is not yet "recovered" in either the biological or legal sense (for further details, see Lockhart and others, this volume).

Conservation activities to assist black-footed ferrets have extended through the past five decades. Included in those activities were three previous workshops and a symposium organized to facilitate interchange of ideas and information. The contents of their published proceedings illustrate changes in emphasis regarding issues important to black-footed ferret recovery. Placing these meetings in a chronological context of major events in ferret conservation (fig. 1) helps to explain motives for convening them and content of the papers, and provides context for the current volume.

The first workshop on black-footed ferrets and prairie dogs (Linder and Hillman, 1973) focused primarily on the rangewide status of the ferret and its prairie dog habitat, with

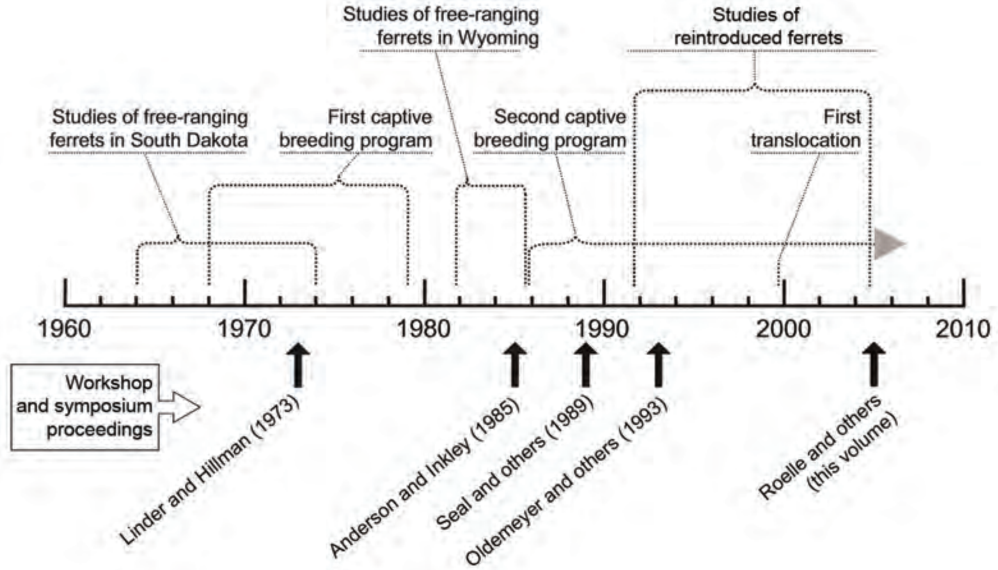


Figure 1. Timeline relating recent symposia and workshops to noteworthy events and periods in black-footed ferret (*Mustela nigripes*) research and recovery.

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a single paper summarizing new information on the biology of the ferret. Despite 10 years of research on the black-footed ferret in South Dakota (fig. 1), Ray Erickson concluded that it remained "one of the least well known of all of the endangered mammals of the United States" (Erickson, 1973, p. 156). Rumors began circulating in the late 1970s that the black-footed ferret was extinct, but these contentions were short-lived because of the discovery of a population of ferrets near Meeteetse, Wyo., in 1981 (Biggins and others, 2006).

The second workshop on black-footed ferrets (Anderson and Inkley, 1985) occurred near the end of a rather brief period of intensive research on the Meeteetse population of ferrets and after the first attempt to captive breed South Dakota ferrets at the U.S. Fish and Wildlife Service's (now U.S. Geological Survey's) Patuxent Wildlife Research Center in Maryland (fig. 1). A single paper in that workshop was devoted to captive breeding, summarizing the failed Patuxent attempt but prophetically predicting success if the venture were to be repeated with ferrets from the Meeteetse population (Carpenter, 1985). The proceedings had a wide variety of other papers on the status of prairie dogs and ferrets, institutional and procedural issues, searches for more ferrets, and research needs. Six papers summarized original field research, much of which was conducted on the Meeteetse population. By summer of 1985, 10 months after the workshop, plague caused extensive declines in the Meeteetse prairie dog population, canine distemper was discovered in the ferrets, and the ferret population plummeted. These events caused an abrupt end to field research on ferrets and forced the beginning of the second captive breeding program following emergency rescue of the remaining animals. Carpenter's (1985, p. 12.11) admonition (presumably motivated in part by his Patuxent experience) to avoid the "tendency to initiate propagation programs as a last resort, when few animals are available for captive breeding" could not be heeded. Research at Meeteetse also served as the primary motivation for publication of a second collection of black-footed ferret papers the following year as number 8 of the Great Basin Naturalist Memoirs (Wood, 1986), although that volume was not the result of a symposium or workshop.

The third workshop, held in 1986, was conceived primarily in response to information needs for the newly developing second effort to maintain and produce black-footed ferrets in captivity (fig. 1). It blended developing theories in conservation biology with existing biological information on ferrets and polecats. This workshop resulted in a book (Seal and others, 1989) with chapters covering systematics, population biology, reproduction, captive propagation, and conservation.

The fourth meeting was a symposium convened in the summer of 1989. Although the captive breeding program had a tenuous beginning (Biggins and others, 2006; Lockhart and others, this volume), evidence predicting ultimate success had emerged by 1988, and thoughts were turning toward planning for reintroduction. Reports in the proceedings (Oldemeyer and others, 1993) focused primarily on habitat for reintroduction of ferrets. Plague received increased recognition as an ominous threat to ferret habitat, with several papers dedicated to discussion of that disease.

The symposium culminating in the papers presented herein was held on January 28–29, 2004, in Fort Collins, Colo. It had been more than 10 years since the previous symposium, and much new information on the biology of the black-footed ferret had been accumulated. Many of the papers published here resulted from information collected as captive breeding became more efficient and as black-footed ferrets were released back into native habitats (fig. 1). The symposium was organized into sections based on the principal topics in the stepdown outline of the Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988). The relationship between the recovery plan and the papers of this symposium illustrates that work is following a somewhat orderly progression guided by principal topics in the recovery plan. A brief description of that relationship introduces each section of this volume.

This volume and the five that preceded it, including proceedings from the three workshops and the symposium, plus the Great Basin Naturalist volume (Wood, 1986), cover a broad spectrum of work on prairie dogs and black-footed ferrets. Although these volumes certainly are not exhaustive in their coverage of ferret and prairie dog research and conservation activities, they collectively provide a solid foundation for future conservationists working with ferrets and chronicle a long-term recovery program for one of North America's most endangered vertebrates.

References Cited

Anderson, S.H., and Inkley, D.B., eds., 1985, Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 1.1–33.12.

Biggins, D.E., Miller, B.J., Clark, T.W., and Reading, R.P., 2006, Restoration of an endangered species—the black-footed ferret, *in* Groom, M.A., Meffe, G.K., and Carroll, C.R., eds., Principles of conservation biology (3d ed.): Sunderland, Mass., Sinauer Associates, p. 581–585.

Carpenter, J.W., 1985, Captive breeding and management of black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 12.1–12.13.

Erickson, R.C., 1973, Some black-footed ferret research needs, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 153–164.

Linder, R.L., and Hillman, C.N., preparers, 1973, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, 208 p.

Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., 1993, Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, 96 p.

Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., 1989, Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, 302 p.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

Wood, S.L., ed., 1986, Great Basin Naturalist Memoirs No. 8: Provo, Utah, Brigham Young University, 208 p.

A Historical Perspective on Recovery of the Black-footed Ferret and the Biological and Political Challenges Affecting Its Future

By J. Michael Lockhart,[1] E. Tom Thorne,[2] and Donald R. (Pete) Gober[3]

Abstract

This paper is a personal commentary by the authors on the background and historical development of the Black-footed Ferret Recovery Program. The black-footed ferret (*Mustela nigripes*) was recognized as imminently endangered in the original Endangered Species Act and has a recovery history accentuated with near catastrophes and remarkable successes. In this paper, we examine the species' near demise, wild black-footed ferret populations, captive breeding efforts, and attempts to restore ferret populations into native habitats. We provide our personal perspectives on many lessons learned during these program stages, the social and political factors affecting species recovery, past and present biological obstacles, and insights relevant to the future of the species.

Keywords: black-footed ferret, captive breeding, endangered species, *Mustela nigripes*, recovery, reintroduction

Introduction

Rather than a technical presentation of data or a literature review, this paper is a personal commentary on historical aspects of the Black-footed Ferret Recovery Program. We offer our recollections and observations only as reflections of our own experiences. We acknowledge that many people contributed to black-footed ferret (*Mustela nigripes*) conservation over this period and that others may view program events and our conclusions differently; however, we submit that our unique positions of program responsibility over the years provide broad perspectives that others not directly involved in day-to-day ferret recovery, or involved in limited areas, may not have gained.

Collectively, as representatives of lead agencies responsible for ferret recovery, we have been directly involved in ferret conservation matters on a daily basis from 1981 to the present. The Wyoming Game and Fish Department (WGFD) was a primary participant in ferret recovery both in the field and in captive breeding from 1981 to 1996 and remains active in reintroduction and program planning activities today. The U.S. Fish and Wildlife Service (FWS) has been involved with ferret conservation since before the species was originally listed as endangered in 1967. Moreover, FWS has been directly involved with captive breeding since 1996 and has coordinated all other recovery activities since that time. In addition, FWS has investigated the likely effects of habitat loss on ferrets as a result of the decline of its principal prey—prairie dogs (*Cynomys* spp.).

In this paper, we discuss ferret conservation activities related to wild population management, captive breeding, and reintroduction into the wild. In particular, we address the significant biological, political, and social issues that affected species recovery. We focus only on the major highs and lows of ferret recovery as we view them; we defer the many important details to other participants in this symposium. Additionally, we characterize our observations of various efforts as successes, failures, or lessons learned. Finally, we provide recommendations linked to these conclusions that may contribute to future recovery of ferrets and perhaps other endangered species.

The opinions and recommendations presented in this paper are those of the authors and do not represent official positions of either the FWS or the WGFD. We also wish to acknowledge the extraordinary dedication, hard work, and contributions accomplished by the many State, Federal, tribal, zoo, and conservation organization partners on behalf of black-footed ferret recovery. Overall program success is the result of enormous efforts by these many program cooperators.

Management of Free-ranging Populations

Ferrets received little attention until the species was listed as endangered in 1967, one of several species to be designated under the first version of the Endangered Species Act (ESA). Early accounts, from Audubon's description of the type

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specimen in the 19th century to anecdotes from rodent control personnel in the mid-20th century, largely treated the species as a novelty. Its secretive and nocturnal lifestyle in remote parts of western North America assured relative anonymity. Conversely, the ferret's principal prey received much more attention: prairie dogs were regarded as vermin, competitors with the agriculture industry, and impediments to western settlement. Accordingly, prairie dog populations were targeted for destruction, and decades of eradication efforts significantly impacted populations of prairie dogs and ferrets, the prairie dog's most highly specialized obligate predator.

Five species of prairie dogs occur in North America. Three of these species cover most of the collective prairie dog (and ferret) historical range: the black-tailed prairie dog (*C. ludovicianus*), the white-tailed prairie dog (*C. leucurus*), and the Gunnison's prairie dog (*C. gunnisoni*). No documented occurrence of ferrets has been linked to either the Utah prairie dog (*C. parvidens*) or the Mexican prairie dog (*C. mexicanus*). These two species have ranges that are relatively small and disjunct from those of the other three prairie dog species. Black-tailed prairie dogs occurred over the largest expanse of land (approximately 160 million ha), from southern Canada to northern Mexico between the 98th meridian and the Rocky Mountains. White-tailed prairie dogs and Gunnison's prairie dogs occurred over approximately 80 million ha to the west of the range of the black-tailed prairie dog. Perhaps 10–20 percent of the range of all of these prairie dog species was physically occupied before western settlement. The actual location of prairie dogs varied with topography, soils, rainfall, fire, bison (*Bison bison*) activity, and other factors. Regardless of the dynamics of these important and variable biological and ecological phenomena, it is obvious that ferrets had an enormous habitat base, and many thousands undoubtedly existed across the landscape.

Ferret populations declined over millions of hectares of occupied prairie dog habitat for three principal reasons. First, a major conversion of native prairie to cropland began late in the 19th century, continued steadily through the Dust Bowl years of the 1930s, and to a lesser extent continues today. Approximately one-third of black-tailed prairie dog potential habitat was rendered useless for prairie dogs by cropland conversion. In comparison, far less of the available habitat of white-tailed and Gunnison's prairie dogs was physically lost to land conversion because, outside of riparian corridors and proximate irrigated lands, much of the habitat occupied by these species is not suitable for crops.

Second, poisoning of prairie dogs as a means of reducing competition with domestic livestock for forage accelerated with agricultural policies in the United States around the time of World War I. Significant Federal funds became available for poisoning programs across the West from approximately 1918 to 1971, after which the use of many of these chemical rodenticides was banned. Tens of millions of hectares of occupied prairie dog habitat were eliminated during this period. Many poisoned prairie dog complexes have never recovered to levels that could support ferret populations.

Third, the exotic disease sylvatic plague, foreign to the evolutionary history of prairie dogs, was inadvertently introduced into North America around 1900. The impact of this disease on prairie dogs and ferrets has been significant. Plague has been documented over all of the ranges of the three principal prairie dog species, except for approximately the eastern third of the black-tailed prairie dog range.

Biologically, the prairie dog ecosystem was devastated by factors described above, and the consequences to ferret populations were even greater. Politically, failure to consider the ramifications of these impacts also resulted in diminished populations of many other species and in several cases led to later consideration of further regulatory protection, such as listings under the ESA. Socially, the domination of farming and ranching activities on most lands in the American West has more severely impacted some species than others. The nadir of occupied prairie dog habitat probably occurred around 1971, when certain toxicants were banned for prairie dog poisoning. Many poisoned prairie dog populations apparently have increased severalfold since that time but remain low relative to historical numbers. Nevertheless, the limited recovery of some prairie dog populations is important in the context of potential ferret recovery and long-range management.

Ferret occurrence undoubtedly mirrored fluctuations in prairie dog populations. Steadily declining numbers of credible ferret sightings occurred during the 1950s and 1960s. The last population of a few dozen animals was thought to have been located in Mellette County, S. Dak., in 1964 (fig. 1). This population was studied through 1974, and a few animals were captured for a captive breeding trial (see below).

Biologically, the initial field studies of wild ferrets in South Dakota provided a starting point for later reintroduction efforts—a small success; however, this population continued to decline in the face of reduced and progressively fragmented habitat. The political will to conserve this individual population through regulatory action did not exist in the era preceding passage of the ESA. This lack of action represented a notable conservation failure inasmuch as, however difficult the challenges of recovering wild populations in native habitat may be, those challenges pale in comparison to the trauma, demands, and resources required for last-ditch captive breeding and reintroduction efforts. Such invasive, intensive recovery programs add many other management dimensions and require more adaptive and risky decisions.

Socially, at the national level, the American public was just becoming aware of the demise of a number of species but had not reacted sufficiently to spur government action to conserve even this last ferret population. At the local level, "business as usual" ranching practices continued to pursue complete eradication of prairie dogs because of their real and perceived competition with domestic livestock. There was little recognition of the ecological importance of prairie dogs and there were no incentive-based initiatives available to conserve this important resource. The lack of understanding and will to maintain viable prairie dog habitats for associated species was a marked failure.

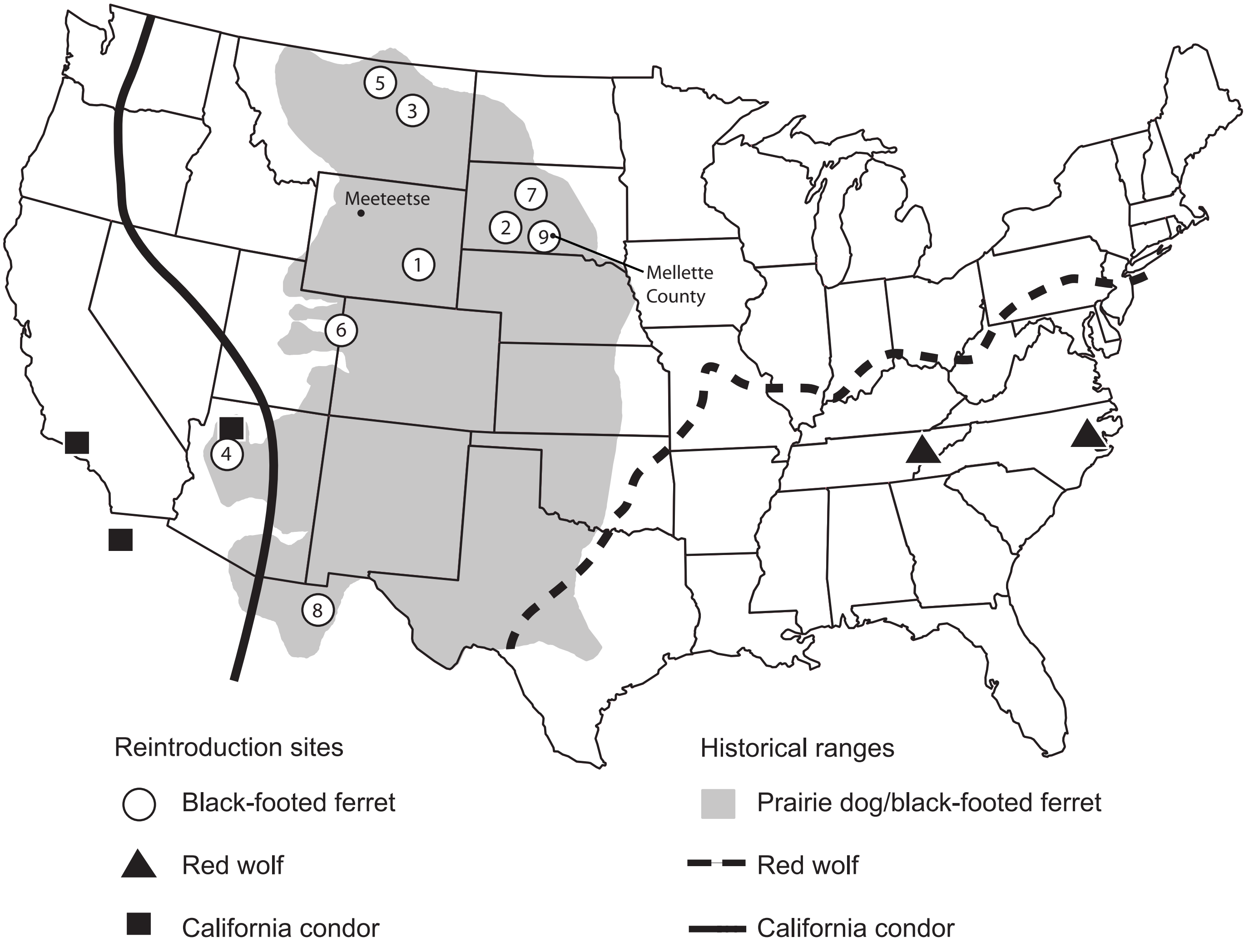


Figure 1. Location of black-footed ferret (*Mustela nigripes*) reintroduction sites overlaid on the collective ranges of three major prairie dog (*Cynomys*) species that are considered their obligate prey. Numbers represent the chronological sequence of ferret reintroductions. Also shown are locations of California condor (*Gymnogyps californianus*) and red wolf (*Canis rufus*) reintroduction sites in relation to their historical ranges.

Are we any more prepared today to deal with such a crisis in a nonregulatory manner? Are means to settle such diametrically opposed concerns readily available if similar circumstances occur again? Unfortunately, we believe the answer to these questions is “no” and reflects another substantial failure in the ability of divergent interest groups, State and Federal agencies, and tribes to find reasonable compromises needed to preserve sensitive species and biological diversity. The inability to find a single ferret in Mellette County, S. Dak., after 1974 was widely regarded at that time as the final demise of the species and must be viewed as a catastrophic conservation failure.

Despite unconfirmed reports, many biologists thought that ferrets were extinct until a ranch dog killed a wild ferret near Meeteetse, Wyo., in 1981. This event ushered in a long recovery process that was widely heralded as a remarkable second chance to conserve a species thought to be lost forever. Intensive attention was focused on this population of over 100 animals (20–40 adults). Considerable field data were acquired from 1981 to 1986 until epidemics of sylvatic plague and canine distemper took a heavy toll on both prairie dogs and ferrets. In hopes of salvaging the species, all remaining wild ferrets were removed from the Meeteetse population between 1985 and 1987 to initiate a captive breeding program.

It must also be acknowledged that underlying social support for endangered species conservation was just beginning to emerge in the 1960s and 1970s. Accordingly, no clear decisionmaking responsibilities were established for ferret recovery during this period, leading to later disputes and second guessing among involved entities. As a means of soliciting advice from experts and interested parties and to help prescribe management direction, WGFD established a Black-footed Ferret Advisory Team (BFAT) in 1982. Considerable acrimony existed within the recovery program during the 1980s and early 1990s, and, although it is never clear when criticism ceases to be constructive, we believe that more assertive and effective leadership by FWS during this period might have helped reduce conflict. We address this issue further in our Summary and Recommendations section.

Despite nearly two decades of extensive and intensive searches, and apart from occasional, unsubstantiated reports, no wild ferrets outside of reintroduction areas have been detected following capture of the last Meeteetse ferret in 1987. Further, we do not believe, given the passage of time and the expansion of plague in western environs, that any undiscovered ferret populations of wild origin exist anywhere in North America today.

With reduced size and quality of prairie dog complexes across most of North America and the presence of plague in many western States, the sustainability of reintroduced ferret populations has also been suspect until very recently. We believe that a wild, self-sustaining ferret population now exists at Conata Basin, S. Dak., and perhaps on Cheyenne River Sioux tribal lands in South Dakota and at Shirley Basin, Wyo. The ability to crop a harvestable surplus of ferret kits from Conata Basin for translocation to other reintroduction areas is a recovery program benchmark of exceptional importance. The Conata Basin ferret population likely represents the largest and most sustainable population that has existed since species listing in 1967, and perhaps for decades before.

Management of wild populations of ferrets (table 1) can be divided into three phases. In comparing these three phases, phase 1, from the mid-1960s to the mid-1970s in Mellette County, S. Dak., ended in disappointment and was greeted largely with resignation. Management efforts during that period were low in intensity and had few available resources. Phase 2, from 1981 to 1987 at Meeteetse, Wyo., was a catastrophe and was largely viewed as a second chance that nearly slipped away. Biological studies at Meeteetse enjoyed considerable resources and were much more intensive, but the existing recovery plan provided little realistic management guidance. Agencies responsible for ferret recovery at that time often disagreed on research and management needs, and required action was sometimes slow to develop. Phase 3, from about the year 2000 and into the future, has a much broader base of support, including a sustainable captive population and multiple reintroduction sites, yet presents new challenges such as habitat improvement needs, genetic management concerns, demographic supplementation in response to adverse stochastic events, diminishing financial resources, and so on. In short, the challenges of continued success now require anticipation of, and responses to, yet unidentified limitations in ferret recovery. Only time will tell whether program collaborators and resources will be adequate to address future uncertainties, but the organizational structure and depth of the recovery program partnership is a successful achievement in its own right and will perhaps ensure more effective responses to any forthcoming environmental or social obstacles.

Captive Breeding

A notable advance in black-footed ferret conservation was the capture in 1971 of six animals from the Mellette County, S. Dak., population for a landmark captive breeding trial. This action was deemed essential because, during the preceding 6 years of field studies in South Dakota, no other black-footed ferret population was discovered nor was any other population known to exist within the ferret's historical range. The 1972 captive breeding attempt was conducted at FWS's (now U.S. Geological Survey's) Patuxent Wildlife Research Center (Patuxent), where management preparations for captive breeding had begun in 1968 with breeding tests of surrogate species (domestic ferrets, *Mustela putorius furo*, and later Siberian polecats, *Mustela eversmannii*). Three additional South Dakota animals were captured and transported to Patuxent for captive breeding in 1972–73.

Efforts to breed black-footed ferrets at Patuxent were crippled from the outset by vaccine-induced canine distemper. Scientists at Patuxent were aware of the susceptibility of domestic ferrets to canine distemper and tested an attenuated distemper vaccine on domestic ferrets to determine safety and efficacy. Although the vaccine was proven safe in domestic ferrets, it induced fatal distemper in four of six vaccinated black-footed ferrets, demonstrating extreme susceptibility to this common viral disease.

Although only nine black-footed ferrets were available for breeding at Patuxent, four of which were lost to vaccine-induced canine distemper, the effort was modestly successful. Two litters of five kits each were born in successive years to a single female. Unfortunately, no kit survived more than a couple of days. The remaining captive ferrets eventually died, and, unfortunately, the breeding research program using surrogate animals was abandoned.

The Patuxent experience demonstrated that black-footed ferrets could be bred in captivity and that captive breeding might be successful if sufficient animals and resources were available. This experience also provided valuable lessons regarding diseases and endangered species recovery. Testing an attenuated vaccine on a surrogate species proved not to be the fail-safe procedure for ensuring vaccine safety for a highly susceptible, highly endangered species. Infectious diseases and their impacts on small populations became obligatory considerations for future recovery of ferrets and other endangered species.

Early ferret recovery efforts at Meeteetse were marred by poor planning, inadequate resources, conflict, controversy, and crisis. Events subsequent to discovery of the Meeteetse population have been, and will continue to be, used as both good and bad examples of endangered species management.

Table 1. Key events in recovery of the black-footed ferret (*Mustela nigripes*).

Year	Wild populations	Captive populations	Reintroduced populations
1964	Small wild population found in South Dakota		
1972		First captive breeding trials at Patuxent Wildlife Research Center, Laurel, Md.	
1974	South Dakota population extirpated		
1979		Last captive from South Dakota dies; species presumed extinct	
1981	Last known free-ranging population discovered near Meeteetse, Wyo.		
1986		First captive breeding effort using Wyoming stock	
1987	Last live ferret removed from Meeteetse; population extirpated	First successful reproduction and weaning in captivity	
1989		First of several additional captive breeding facilities established	
1991			First reintroduction: Shirley Basin, Wyo.
1994			Second and third reintroductions: Conata Basin/Badlands, S. Dak., and southern Phillips County, Mont.
1996			Fourth reintroduction: Aubrey Valley, Ariz.
1997			Fifth reintroduction: Fort Belknap, Mont.
1999		Captive population objective established in Species Survival Plan® reached; captive population considered stable	Sixth reintroduction: Colorado/Utah border
2000	First reintroduced population with harvestable surplus of kits for translocation to other sites		Seventh reintroduction: Cheyenne River Sioux tribal lands, South Dakota
2001			Eighth reintroduction: Janos, Chihuahua, Mexico
2002	Wild ferrets exceed captive ferrets in number		
2003			Ninth reintroduction: Rosebud Sioux tribal lands, South Dakota

Black-footed ferret recovery efforts in the 1980s and early 1990s were highly scrutinized and frequently criticized, often by individuals uninformed about recovery events and/or Federal and State laws regarding endangered species management. Although some reviewers and participants were well-intentioned and constructive, others ignored difficult problems and overlooked lessons learned in earlier ferret recovery efforts and other endangered species programs.

The Black-footed Ferret Recovery Plan of 1978 was written at a time when ferrets were thought to be extinct, and it provided little or no effective guidance for management of the Meeteetse population. In March 1982, WGFD quickly formed the aforementioned BFAT. This multiagency and private sector committee provided advice and guidance to WGFD in determining management direction for the Meeteetse population. Black-footed ferret numbers at Meeteetse increased from discovery in 1981 through 1984, when the population comprised approximately 40 adults and 90 juveniles. Based on this somewhat robust population and because no other wild population had been found (despite increased interest and improved search techniques), WGFD and FWS jointly decided in May 1985 to capture a small number of black-footed ferrets the following fall to begin a modest captive breeding trial. The WGFD's Sybille Wildlife Research and Conservation Education Center (Sybille) near Wheatland, Wyo., was selected as temporary quarters for captured ferrets. Ultimately, knowledge gained from Patuxent was used to develop technology and facilities at Sybille to support a long-term captive breeding program that would eventually provide animals for reintroduction and protect the species from extinction in the event of an unexpected catastrophe at Meeteetse.

The decision to initiate a captive breeding program did not come easily or without conflict. It took optimism generated by the high number of black-footed ferrets documented in the fall of 1984 and assurances that funding would be supplied by FWS in 1986 or 1987 for WGFD to commit to captive breeding. Although captive breeding was started less than 4 years after discovery of the Meeteetse population, in hindsight it should have been started earlier. The delay is understandable, however, and can be largely attributed to uncertainties in the availability of funding and suitable facilities and to the fear of animal loss and breeding failure. Lessons learned through this process were twofold: captive breeding of critically endangered species should be initiated early, and adequate advance planning and committed funding for personnel and facilities are essential. These lessons are not unique to the black-footed ferret program and were applicable to other endangered species, including the red wolf (*Canis rufus*) and California condor (*Gymnogyps californianus*).

The importance of these lessons became evident in the summer of 1985, even before the first attempts to capture ferrets for breeding. In June 1985, sylvatic plague was identified in Meeteetse prairie dog colonies. Sylvatic plague usually causes extensive die-offs in affected prairie dogs. In an attempt to halt the disease episode (by killing flea vectors of plague), FWS and WGFD conducted a massive plague-control program and dusted approximately 80,000 prairie dog burrows with the insecticide carbaryl. Nevertheless, the epizootic reduced Meeteetse prairie dog colonies by about 20 percent in the first year. Although the susceptibility of prairie dogs to sylvatic plague was well known, at that time black-footed ferrets were thought not to be susceptible. Siberian polecats, domestic ferrets, and other mustelids and carnivores are largely immune to sylvatic plague. Several years later, it was discovered that black-footed ferrets are actually exceptionally sensitive to plague. Black-footed ferret numbers at Meeteetse declined sharply over the summer of 1985, and only 58 animals were documented by August.

In September and October 1985, six ferrets were captured for captive breeding trials and moved into temporary quarters at Sybille. These captures led to discovery of another cause of the decline of ferret numbers at Meeteetse. One of the last two animals trapped died from canine distemper, an illness undoubtedly contracted before capture. Based on the experience at Patuxent with vaccine-induced canine distemper and the highly contagious nature of this disease, it was predicted that the remaining black-footed ferrets originally transferred to Sybille would succumb to the disease, which proved true. It was also predicted that most, if not all, animals in the free-ranging population at Meeteetse would be lost. Although extensive precautions had been taken to prevent introduction of diseases from outside sources, no precautions were taken to guard against known ferret diseases within the free-ranging colony. Another lesson learned.

At that point, management of the free-ranging black-footed ferret population and the fledgling captive breeding program were thrown into crisis. Given the reduced numbers of ferrets, it was unlikely that simultaneous efforts to maintain a wild population and start a captive breeding program would succeed; given the presence of disease, it was questionable whether a wild population could realistically be preserved. The WGFD, an agency accustomed to managing free-ranging wildlife, quickly, but with difficulty, decided to begin a second capture effort to obtain founders for captive breeding. This action was taken with recognition that it would likely lead to extirpation of the wild population. Interestingly, opposition to this second capture effort came primarily from individuals who disagreed with human interference and felt that black-footed ferrets should be allowed to go extinct.

In October and November 1985, six more ferrets were captured and placed in strict isolation quarters at the University of Wyoming until it was certain that all were free of canine distemper. Capture efforts were halted in late fall in the hope that any free-ranging black-footed ferrets remaining at Meeteetse would breed in the wild. Also during this period, WGFD invited the Conservation Breeding Specialist Group (CBSG) of the Species Survival Commission of the International Union for the Conservation of Nature and Natural Resources to provide expert advice on developing a captive breeding program.

Captive ferrets did not breed during the 1986 season, probably because of male immaturity and stresses associated with capture and a captive environment. Recovery partners experienced especially difficult times in 1985 and 1986. The responsible agencies received pointed and outspoken criticism; accusations ranged from allegations of mismanagement to intentional exposure of ferrets to canine distemper. Conflicting recommendations were received, including capturing all free-ranging black-footed ferrets immediately, removing captive animals from WGFD's care and terminating its role, curbing all further management intervention in the fate of the wild population, and so on. In spite of stresses, alliances between WGFD, FWS, and other recovery partners began to solidify.

Five free-ranging black-footed ferrets survived the canine distemper epizootic at Meeteetse, and two females subsequently produced litters in the spring of 1986. According to a contingency plan prepared by WGFD with assistance of CBSG and approved by FWS, the WGFD decided in August 1986 to capture all remaining animals. The last of 12 known wild black-footed ferrets was trapped in February 1987, and all captured ferrets were taken to a newly completed captive breeding facility at Sybille. The free-ranging black-footed ferret population at Meeteetse was thus extirpated, and the remaining captive individuals became one of the most endangered mammals in the world, as well as the last hope for the species. Survival and future recovery of the black-footed ferret now depended on development of an effective captive breeding program, which at that time had no proven track record.

Events from October 1981 through early 1987 occurred rapidly and developed in the absence of a current or applicable recovery plan, but critical decisions were still necessary. Perhaps issues faced by WGFD, FWS, BFAT, and CBSG could have been better anticipated and addressed, including analysis and consideration of probabilities of extinction of the small Meeteetse black-footed ferret population; when and how to best initiate captive breeding efforts; how to fund captive breeding; potential responses to epizootics of canine distemper and sylvatic plague; when and how to remove the last free-ranging animals to prevent extinction; appropriate responses to discovery of another wild ferret population; and advance identification and preparation of suitable reintroduction sites.

By spring of 1987, with funding assistance from FWS, the captive black-footed ferret colony was moved into permanent facilities at Sybille. With the assistance of CBSG and the University of Wyoming, WGFD improved captive husbandry protocols, began a genetic management plan, and began intensively monitoring black-footed ferret reproductive cycles and pairing events. Captive breeding techniques were developed with the intent of minimizing stress and injury and maximizing longevity, productivity, and genetic contribution of founder animals without promoting domestication. Two litters were born, and seven kits were weaned in 1987. Production of these kits was exceptionally significant, not because of the number of kits weaned or their genetic makeup but because it was finally demonstrated that black-footed ferrets could be bred and reared successfully in captivity.

The CBSG, WGFD, and FWS held a workshop on black-footed ferret conservation biology in 1986. A captive breeding program plan (*A Strategic Plan for the Management of Black-footed Ferrets in Wyoming*), with time-specific objectives, was written in 1987. This plan recognized that few animals were available for captive breeding and that many were related. It called for maintaining approximately 90 percent of the original genetic heterozygosity of founder ferrets over a relatively short period of 50 years. This would be accomplished by establishing a captive population of 500 animals with a stable age and sex distribution, which would provide an effective population of about 250 ferrets and approximately 200 breeding-age animals. During the early stages of the program, increasing the population had priority over managing genetics. Subsequently, ferret pairings were planned to maximize retention of founder alleles.

Another objective of the strategic plan was to raise enough animals to establish a second geographically removed population to protect the species from catastrophic loss. The two-facility objective was reached in 1988 when a few ferrets were moved from Sybille to the Henry Doorly Zoo, Omaha, Nebr., and the National Zoological Park's Conservation & Research Center, Front Royal, Va. Demographic and genetic data were maintained in a detailed studbook. Separate captive populations were genetically managed and bred as a single population. The strategic plan also called for initial ferret reintroductions to begin in 1991, provided that the captive population reached 500 animals with 200 breeding-age adults.

A revised Black-footed Ferret Recovery Plan was completed by FWS in 1988. It included most of the goals of the Wyoming strategic plan and called for ensuring immediate survival of black-footed ferrets by increasing the captive population to 200 breeding adults by 1991. Additionally, it included a downlisting goal of establishing a prebreeding population of 1,500 free-ranging, breeding-age ferrets in 10 or more populations, as widely distributed as possible over the historical range, by the year 2010.

Over the next few years, additional captive populations were established at the Cheyenne Mountain Zoo, Colorado Springs, Colo.; the Louisville Zoo, Louisville, Ky.; the Metropolitan Toronto Zoo, Toronto, Ontario, Canada; and the Phoenix Zoo, Phoenix, Ariz. The contribution of these zoos to ferret recovery was enormous. They received no monetary support from WGFD or FWS and initially were not allowed to use ferrets for exhibit. Another requirement was that participating zoos be accredited by the American Zoo and Aquarium Association (AZA), which had established a program to develop Species Survival Plans® to facilitate captive breeding of endangered and declining species. With growing involvement of AZA zoos and maturation of the captive breeding program in 1989, the technical advisory role previously filled by CBSG was vested in AZA through an established Black-footed Ferret Species Survival Plan (SSP) and associated Management Group of facility specialists.

The partnership between the AZA's SSP, WGFD, and FWS was, and remains, successful, and black-footed ferret recovery has benefited greatly from this relationship. Participants in the Black-footed Ferret SSP Management Group included representatives from involved zoos, WGFD, and FWS, as well as numerous outside advisors who provided extensive expertise in husbandry, veterinary care, disease, reproductive management, population management, and genetics. The commitment of the SSP Management Group, CBSG, and their many advisors was rewarded in 1991 when captive-bred black-footed ferrets were first reintroduced into the wild at Shirley Basin in central Wyoming.

With expansion of the reintroduction phase of black-footed ferret recovery to sites outside Wyoming, and with dwindling financial resources within WGFD, management responsibility for the Sybille captive breeding facility shifted to FWS in 1996. The breeding facility is now part of the National Black-footed Ferret Conservation Center and has moved to a new site in northern Colorado. The new facility became operational in the fall of 2005.

A review of the Black-footed Ferret Recovery Program, with particular attention to captive breeding elements, was undertaken by AZA in 1995, and a similar analysis and update was accomplished by CBSG in 2003. These critical reviews of the history, progress, and operations of captive breeding projects have been instrumental in evaluating problems and providing important input into the direction and management of captive breeding.

Beginning in 1997, an effort was undertaken to increase overall captive production and kit quality for reintroduction purposes. Ferrets excess to the SSP were used to develop limited field breeding projects in association with reintroduction efforts in Arizona, Colorado, and Montana. A separate field breeding facility (no accompanying reintroduction effort) was constructed near Raton, N. Mex., by the Turner Endangered Species Fund. Although many of the basic SSP husbandry and breeding procedures were employed, these projects were initially designed to test more hands-off breeding strategies in outdoor pens with well-developed prairie dog burrow systems. Breeding success at these facilities has been mixed and has varied substantially between sites. In addition, the expense of operating pen breeding facilities has often been greater than anticipated and, as a consequence, has affected other elements of reintroduction projects. The objective of increasing production and potentially improving the survival of released ferrets, however, remains a guiding principle of the recovery program and has been a recurring recommendation in all formal program reviews. Additional evaluation and refinements of pen breeding capabilities warrant further attention.

Although the black-footed ferret captive breeding program will continue to evolve, it has been a great success: the first animals were captured for captive breeding 4 years after discovery of the Meeteetse population; the program survived the sylvatic plague and canine distemper crisis of 1985 and extirpation of the species in the wild by 1987; and the first experimental reintroduction occurred just 6 years after the first animals were captured to initiate captive breeding. The captive breeding program has produced and weaned over 4,800 ferrets (through 2003) and has supported several reintroduction efforts across the former range of the species. In addition, the program has provided animals for essential disease and vaccine research, for survival enhancement, and for educational exhibit. For the foreseeable future, black-footed ferret recovery hinges on the continued success and management of the captive population by involved agency and zoo partners.

Reintroduction

With increasing success in black-footed ferret captive breeding efforts in the late 1980s, recovery program partners focused greater attention on restoring wild ferret populations. Initial interest was directed at reestablishing a ferret population at the site of their last wild origin near Meeteetse, Wyo., but sylvatic plague substantially reduced overall habitat quality on the Meeteetse prairie dog complex, thus rendering the site unsuitable for ferrets. Today, prairie dog populations in the Meeteetse area are still depressed, which highlights a serious obstacle to ferret recovery. In the absence of effective plague intervention and management capabilities, many affected prairie dog colonies may never regain historical population levels and may never support viable ferret populations. This issue is discussed at greater length below.

The primary goal of the black-footed ferret recovery program is to reestablish a sufficient number of viable, wild ferret populations in order to downlist and recover the species, remove it from ESA protections, and terminate the expensive captive breeding program now necessary to support species survival and recovery efforts. Between 1991 and 2003, 12 discrete reintroduction projects were initiated at nine reintroduction areas in six western States (Arizona, Colorado, Montana, South Dakota, Utah, and Wyoming) and at one site in northern Chihuahua, Mexico (fig. 1). The history and results of these specific reintroduction efforts are addressed elsewhere and will not be detailed here. Instead, we highlight overall direction, research, monitoring efforts, ferret survival, and success in general terms and from our personal views and recommended direction.

As of 2003, over 1,800 ferrets had been reintroduced into the wild. Success of these efforts, in terms of establishing self-sustaining populations, has been mixed and affected most significantly by habitat suitability (which, in turn, is most affected in recent years by the presence of sylvatic plague throughout most of the historical ranges of prairie dog species and ferrets). Only in South Dakota do large, relatively contiguous, and plague-free prairie dog complexes remain, and the greatest reintroduction success to date has been at the Conata Basin site (Buffalo Gap National Grasslands) in south-central South Dakota. Conata Basin experienced exponential growth in the wild ferret population following only 3 years of reintroduction and a total release of 165 captive animals. Ferrets at Conata Basin may have spread through most of the available habitat and are possibly approaching population saturation levels, having produced a relatively consistent 60 to 70 litters annually over the past 3 years. Conata Basin is the only site to have reached a success level that allows translocation of wild-born kits to other reintroduction sites, and kits from Conata Basin have been used to support reintroductions in Colorado and at two other sites in South Dakota. Similar successes are expected at two more recent South Dakota reintroduction sites that also support relatively large, plague-free prairie dog complexes (Cheyenne River Sioux and Rosebud Sioux tribal lands). In contrast, plague has been documented either in or around five of the other reintroduction areas outside of South Dakota.

To date, there have been six reintroduction projects in black-tailed prairie dog habitat (Montana, Mexico, and South Dakota), two in white-tailed prairie dog complexes (central Wyoming and an area straddling the Colorado/Utah border), and one in Gunnison's prairie dog habitat (northwestern Arizona). Differences in prairie dog colony size, density, and life history (e.g., hibernation) exist both between and within species (over the extent of each species' range) and undoubtedly influence site quality and success of ferret reestablishment. For the most part, black-tailed prairie dogs currently occupy definable "towns" of varying size (but historically included enormous colonies), exist at greater densities, and typically do not undergo extended torpor. On the other hand, Gunnison's and white-tailed prairie dogs are more scattered and less dense over areas they occupy and hibernate for extended periods.

Other regional factors such as geography, vegetation, annual precipitation, and drought also affect site suitability and reintroduction potential. Land ownership patterns, land use, access, and vehicle use constraints further affect implementation and monitoring efficacy of reintroduction projects. As a consequence of such dynamics, the recovery program has experienced both outstanding and rapid reintroduction success, as well as projects that have struggled to maintain even minimal populations. Still, no reintroduction project is regarded as a failure, and all have provided vital experience and information to help foster ongoing and future recovery efforts across the ferret's historical range. Moreover, given the severe limitations in available reintroduction sites in North America today, it would be imprudent to give up on any reintroduction area that has the necessary land base and potential for improved habitat conditions and ferret recovery.

Only ferrets considered excess to the captive population have been used to support reintroduction projects. The captive, SSP population is regarded as the essential foundation of the species today. And with the exception of ferret releases in Mexico, all reintroductions have been accomplished under a special provision of the ESA (section 10(j)) that provides for designation of reintroduced populations as "nonessential, experimental." Ferrets released into nonessential, experimental population areas (as established via Federal rulemaking and ESA consultation procedures) are no longer classified or managed as endangered but are given protection and management flexibility similar to that provided for "candidate" species (candidates for listing under ESA but not yet listed). This relaxed management flexibility was necessary to gain the support of State governments and private landowners for releases of an endangered species into areas with fragmented ownership patterns of public and private lands.

The section 10(j) nonessential, experimental provisions facilitated ferret reintroduction trials; it is unlikely that most projects would have been successfully implemented without 10(j) or a similar mechanism to reduce the perceived consequences of potential expansion of endangered ferrets onto private lands. The nonessential, experimental designation has other limitations that impede ferret recovery, however, and a review of the utility of 10(j) and reexamination of other options to tailor reintroductions to site-specific situations are warranted. More discussion is provided below.

With the recovery program becoming more focused on reestablishing wild ferret populations in the early to mid-1990s, other forms of partner acrimony began to surface. Disputes over "soft" versus "hard" release techniques, ferret preconditioning and predator avoidance training, predator control, use of radio telemetry to document survival, how and where to prioritize excess ferrets for release, State versus Federal authorities, and other research issues, some of which first began to surface during the Meeteetse era, seemed to deepen divisions among some participants.

Despite individual and agency conflicts and occasional setbacks, a committed partnership of biologists and administrators set aside differences (or, perhaps more accurately, worked around them) to focus attention on biological and social impediments to ferret recovery. As a consequence, reintroduction efforts continued to gather momentum between 1991 and 2003, and a wealth of information was gathered over that period about how to effectively reestablish ferret populations and respond to obstacles.

Also, the recovery program experienced a somewhat unexpected and positive turnaround in the status of two reintroductions over the past several years. Reintroductions at Shirley Basin, Wyo., were suspended in 1994 because of an extensive plague outbreak. Subsequent monitoring suggested that the small remaining ferret population was likely to be lost by the end of the 1990s; however, starting in 2002, the Shirley Basin population exhibited its own exponential growth and appears to be rapidly developing into a self-sustaining population. Prairie dog populations in Shirley Basin are also rebounding. Likewise, wild ferret production at Aubrey Valley in northwestern Arizona has recently increased following years of reintroduction attempts, probably as a result of spring ferret releases (releases designed to place ferrets in the wild when they can best exploit prairie dogs emerging from hibernation and young pups).

Perhaps one of the most significant findings from the early reintroduction development stages was recognition of the importance of preconditioning captive ferrets prior to release in the wild and an associated partner commitment to expand preconditioning capacity by constructing a number of outdoor facilities at or near reintroduction sites in Arizona, Colorado, Montana, New Mexico, and South Dakota. In simplest terms, preconditioning is the exposure of captive-produced ferrets to a more natural outdoor environment with relatively large pens, prairie dog burrow systems, and live prairie dog prey. In these pens, cage-reared ferrets become accustomed to the security and life needs of prairie dog colonies; essentially, they learn to behave like wild ferrets. As addressed above, outdoor pen facilities in Arizona, Colorado, Montana, and New Mexico were also used to conduct experimental breeding trials to increase the number of animals available for reintroduction.

Certainly, much has been learned about reintroducing ferrets. Still, many pressing uncertainties remain, particularly those dealing with management of ferrets in plague-affected environs, and additional research and reintroduction trials are warranted. And perhaps one of the best ways to speed recovery is to “cast a wide net” by placing ferrets in as many potential sites as possible and letting ferrets ultimately reveal what constitutes favorable habitat and management conditions.

As noted above, in 1995 the AZA was contracted by FWS to conduct a comprehensive review of the ferret recovery program. In this review, the AZA examined the status and success of captive breeding and reintroductions, as well as the administration and general decisionmaking procedures of the program. Much of the information was gathered through a series of partner workshops. A final report to FWS in 1996 included many valuable and specific recommendations on the biological and administrative needs of the recovery program. With waning funding in WGFD and expanding recovery efforts beyond the State of Wyoming, in 1996 FWS assumed primary responsibility for operation of the Sybille breeding facility and management of captive and field recovery activities. Following guidance provided in the AZA report and as set forth in ESA, FWS also established the Black-footed Ferret Recovery Implementation Team (BFFRIT) in 1996 and invited participation of agencies, organizations, and tribes directly involved in ferret recovery activities.

The BFFRIT replaced the original BFAT and subsequent Interstate Coordinating Committee as the vehicle for maintaining partner coordination and input into recovery program direction. The BFFRIT is composed of 26 cooperating State and Federal wildlife and land management agencies, tribes, zoos, conservation organizations, and the National University of Mexico. The BFFRIT charter established the Executive Committee (administrators of agencies/organizations who address recovery program policy and funding issues), the Conservation Subcommittee (composed of technical experts to deal with field reintroduction and research elements), and the Education Outreach Subcommittee (to expand public awareness of the recovery program and help pursue outside funding opportunities). The SSP Management Group, established originally by the AZA in 1991 and made up principally of zoo representatives, also effectively serves as a technical subcommittee to the BFFRIT and provides input and expertise on management of captive breeding programs.

Although FWS retains ultimate authority, the BFFRIT provides essential input and recommendations on all matters related to ferret recovery and has effectively guided program direction since its inception. To establish more balanced and objective procedures for allocating ferrets for reintroduction and research purposes, FWS (through the BFFRIT) also developed an annual ferret allocation and project evaluation process in 1996. This allocation process sets priorities for ferret distribution based on the biological suitability of proposed release sites, overall project and/or research merit, and potential recovery program benefits. Allocation proposals, which provide details on habitat attributes of project areas, disease and predator presence and management capabilities, project/research design and implementation capabilities, and so on, are submitted to FWS by mid-March each year. The proposals are then distributed to BFFRIT members for review.

The FWS awards a preliminary ferret allocation in late May via a report that fully discloses (albeit anonymously) comments and recommendations provided by BFFRIT members and a justification of FWS findings. The number of ferrets identified in the preliminary allocation is determined from an expected production level based on a 5-year average recruitment rate from the number and age distribution of female ferrets presently in the SSP-managed population. For now, and into the foreseeable future, first priority for ferrets goes to SSP facilities to maintain the genetic representation and viability of the essential captive population. Final allocation decisions are made in late summer and depend on the actual production achieved by SSP facilities and field breeding projects, as well as on resolution of any permitting or other project implementation deficiencies (e.g., funding, partnership commitments).

The current organizational structure of the Black-footed Ferret Recovery Program has had the benefit of time, conflict, and critical analysis to evolve. Fortunately, ferrets have persisted during periods of unforeseen crises and human mistakes. The BFFRIT is a product of important lessons learned over the history of the ferret program, and we believe it offers a good example of an effective strategy for management of large, complex, endangered species recovery programs. Instead of a typical, more academically based and smaller recovery team, a recovery implementation team provides a transparent decision process and equal voice to a large number of involved agencies, tribes, and organizations. Although FWS retains ultimate authority and responsibilities as specified in the ESA, the BFFRIT is relied on to help make informed program decisions, help resolve partner disagreements and other program conflicts, and generally keep recovery efforts moving in a positive direction. We regard such continued partner participation as essential to successful recovery of the black-footed ferret.

Finally, the most pressing limitation to ferret recovery is availability of suitable habitat to restore and support wild populations. Although program partners have always understood that habitat availability is key to recovery, other program imperatives between 1985 and 1997 (i.e., development of captive breeding and reintroduction capabilities) somewhat diluted focus on habitat issues. In 1998, the BFFRIT Conservation Subcommittee was tasked to identify and prioritize the top 10 sites that could support ferret reintroduction across North America, as well as secondary areas that could possibly be developed into additional reintroduction sites. In 1988, only 10 years earlier, an internal FWS document suggested that as many as 38 suitable ferret reintroduction areas existed in the United States. That document was based solely on suggestions from program partners and did not attempt to accurately assess current prairie dog populations, complex size and quality, the status of plague, or other practical biological and political factors (e.g., land ownership patterns) necessary to determine reintroduction potential.

With more detailed surveys of BFFRIT partners, the 1998 assessment of site potential indicated that only nine sites could immediately support ferret reintroductions across North America. Five of these sites were already engaged in reintroduction projects, and three more were activated between 1998 and 2003. Since 1998, a few other potential release areas have been identified, but it is clear that prairie dog habitat throughout the historical range of the ferret has been so severely degraded that ferret recovery is not feasible without restoration of large, healthy prairie dog complexes.

What constitutes a suitable prairie dog complex for ferrets is a question still under scrutiny by program partners and is a pertinent issue to be addressed in an upcoming and long overdue revision of the Black-footed Ferret Recovery Plan. In examining the results of reintroduction efforts to date, the only relatively large, self-sustaining, wild population of ferrets (ca. 250–400 animals) is at Conata Basin, a site that contains some 6,070 ha of closely distributed and relatively dense black-tailed prairie dog colonies—prairie dog colonies that are also free of sylvatic plague and are managed to preserve high prairie dog habitat values. Although prairie dogs of all three species are well dispersed throughout their former ranges, prairie dog complexes are very small and highly fragmented compared to historical conditions. There are very few places within North America that approximate the quality of habitat for ferret recovery exhibited at Conata Basin.

The revised Black-footed Ferret Recovery Plan (published by FWS in 1988) sets forth a downlisting objective by the year 2010 of 1,500 adult (breeding) ferrets, established in no less than 10 separate populations across the historical range of the ferret, with at least 30 individuals in each population. Although a prebreeding census of 1,500 adult ferrets may be attainable with continued recovery success in the few large prairie dog complexes that exist, there appear to be only four or five sites today that have the potential to support viable ferret populations, the majority of which will likely be in plague-free complexes in South Dakota.

Future recovery of the black-footed ferret hinges on our ability to successfully reintroduce and reestablish relatively large, healthy populations in the wild. Unlike two other endangered, high-profile carnivores of the West, the gray wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*), the entire breadth of habitat within the ferret's historical range has been materially impacted: there are few large expanses of Federal public land with sufficient prairie dog habitat to support black-footed ferret populations at the present time. Furthermore, although the amount of land potentially available for habitat restoration across the historical range of the ferret far exceeds potential capabilities for two other critically endangered species, the California condor and red wolf (fig. 1), there are significant social and political impediments to restoring and managing large blocks of grasslands for prairie dogs and ferrets. Prairie dogs are still largely regarded as vermin by private landowners and agricultural interests, and only small, relatively fragmented complexes are typically tolerated, if at all.

And so, ironically, we appear to be at yet another important crossroad for this species. Having brought the ferret back from the brink of extinction, having invested enormous national resources to right an ecological wrong, and having developed the necessary capabilities and expertise to actually recover this species, the future of the ferret hangs on our social and political will to set aside and develop sufficient habitats that could be managed for prairie dogs, ferrets, and other sensitive prairie wildlife species. Ferret recovery efforts have come full circle, and it will be an enormous challenge to overcome a prevailing attitude of “not in my backyard” when so few suitable, welcoming backyards are presently available.

Summary and Recommendations

Given the status of the ferret in 1987, when only 18 live animals remained, we submit that ferret recovery has been one of the most successful endangered species programs to occur anywhere, at any time. Table 2 compares several recovery parameters for three well-known North American species that were listed as endangered in 1967. The black-footed ferret, California condor, and red wolf are notable “grandfathered species” that have always been included in the various versions of ESA. Each became further imperiled after listing, and each was subsequently removed from the wild for captive breeding and eventual reintroduction. Figure 1 indicates the historical range of these species and the sites where reintroduction has occurred. Clearly, the “recovery glass” is potentially “half full” for the ferret compared to species that mature less quickly, have fewer young, and whose range and essential habitats have been even more drastically altered.

The lessons taught by ferrets, condors, and red wolves should be carefully heeded. Reducing any species to such critically low population levels that captive breeding becomes the only possible recovery strategy is a poor way to ensure persistence, much less recovery. Extinction risks are elevated, recovery becomes more expensive, and bringing species into captivity may remove assurances that adequate habitats will be available for later reintroduction.

Table 2. Comparisons of some recovery parameters for three North American endangered species removed from the wild, propagated in captivity, and reintroduced into their historical ranges, 1967–2003.

	Black-footed ferret (***Mustela nigripes***)	**California condor** (***Gymnogyps californianus***)	**Red wolf** (***Canis lupus***)
Year species listed	1967	1967	1967
Year extinct in wild	1987	1987	1980
Number removed from wild	18	27	17
Initial number used in breeding	7	14	14
Number propagated in captivity to date	4,800+	283	727
Number held in captivity, breeding	~400	130	300
Year reintroduction began	1991	1992	1987
Number reintroduced to date	~1,800	~167	~120
Number of attempted reintroduction sites	9	7	2
Number weaned or fledged in wild	~1,200	1	289
Number in wild	~600	~80	~100
Reintroduction sites, likely viable	3	0	1
Reintroduction sites, not viable	2	0	1
Reintroduction sites, unknown viability	4	7	0

The ferret recovery program has experienced a number of successes, failures, and hard-learned lessons over the years. It is important to continually characterize progress so the direction and speed of recovery can be adjusted accordingly. Overall, we believe that the ferret recovery program will probably continue to be successful, despite many near disasters and remaining obstacles. Ferret recovery efforts may be compared internally by contrasting results of different activities over time. Comparisons of the progress and success of other endangered species recovery efforts may also provide perspective that will aid ferret recovery.

To date, we believe that (1) black-footed ferret captive breeding has been highly successful, (2) ferret reintroductions have achieved a low to moderate degree of success, and (3) wild population management has experienced a low degree of success. Marked improvements and efficiencies have occurred in all of these areas over the last decade, however.

The most notable success of captive breeding has been the creation of a mutually supportive network of staff and facilities that successfully raise animals in a protected environment to ensure species survival and provide animals for reestablishment of wild populations. Problems that have occurred in this recovery component have been straightforwardly addressed. One nagging limitation that may or may not be possible to fully overcome in a captive environment is the relatively low whelping success in females (as compared with wild whelping rates). The most important lesson learned over the course of the ferret program, however, is that biological breakthroughs in complex recovery efforts can only be realized via the successful involvement of many diverse partners.

Ferret captive breeding may become more efficient as limitations are identified and addressed, but this recovery component is mature, with over 15 years of accumulated experience. Most attainable internal refinements may already have been achieved. If increased numbers of animals are required for reintroduction, it may be most practical simply to increase the number or size of facilities. Captive breeding of ferrets is a tightly controlled process with few extraneous factors affecting its continued success or failure. Extended captivity may reveal future biological constraints (e.g., inbreeding suppression), but most political and social obstacles to captive breeding appear to have been adequately addressed.

At present, the knowledge and resources needed for continued success of the captive breeding program appear to be in place. Nevertheless, we recommend that continued and rededicated attention to partner coordination and involvement be nurtured through the SSP Management Group and BFFRIT. Although this recommendation may appear gratuitous given present successes, renewed emphasis is essential to address a crucial, laborious, and continuing program element whose failure would undercut all other recovery activities. A recurring error of many recovery efforts is to gradually pay less attention to successful foundation components when new limiting factors are identified.

Likewise, progress in reintroducing ferrets and establishing viable, wild populations requires continued nurturing of program cooperators and development of new partnerships with other States across the ferret's historical range. The most notable success of the reintroduction component has been the relatively rapid involvement of the few suitable sites for active releases, but few large, high-quality prairie dog complexes remain, and future recovery depends on both short-term and long-term habitat restoration. In concert with renewed efforts to identify and enhance potential recovery habitat, new reintroduction trials and continuing research to refine vaccines and develop other possible disease management capabilities are also essential.

The most notable accomplishment of wild population management has been the apparent sustainability of at least one reintroduced population. The ferret population at Conata Basin, S. Dak., is believed resilient enough to withstand harvest of surplus animals for translocation to other reintroduction sites. This is a remarkable accomplishment and indicates a population likely more stable than any other extant population during the last half century.

The review of the Black-footed Ferret Recovery Program by CBSG in June 2003 and the subsequent report issued by CBSG in January 2004 provided many practical recommendations to further ferret recovery and addressed issues and program needs related to captive breeding, reintroduction, disease, and habitat. Many of our views and recommendations echo information contained in the CBSG report; however, given the current status of the recovery program, after almost 20 years of captive "life support" for the ferret, and the prospect of a difficult recovery future (given habitat limitations), perhaps other, more fundamental questions need to be asked and other key recovery priorities more fully pursued.

To realistically fulfill our recovery mission, how do we secure greater commitments for financial resources, private land incentives, and public land-use reforms necessary to set aside, develop, and sustain sufficient habitats across the historical range of the ferret?

Given the presence of plague in the environment and the timetable likely necessary to restore suitable prairie dog complexes, a foundation of available sites needs to be identified and attendant implementation strategies and schedules prescribed in a timely manner. It may take 10–20 years of intensive management to enhance complexes of prairie dog habitat to the point that they can support healthy ferret populations; planning and commitments must start soon. Federal public lands (national grasslands, Bureau of Land Management property, national wildlife refuges, national parks and monuments, and military lands) should bear a disproportionate amount of habitat development. Responsibilities under section 7(a)(1) of the ESA (a provision requiring all Federal agencies to fully promote and support endangered species recovery) should be reinforced at the national level, both with funding and refocused priority, to establish and manage large prairie dog complexes wherever possible. Partnerships with tribes and private land owners must be pursued to secure recovery areas over those portions of the ferret's historical range where public lands are largely absent. Cooperative efforts with Canada and Mexico should continue in order to develop recovery sites at the northern and southern extents of the ferret's historical range.

How can administrative procedures be improved to more effectively and rapidly develop suitable black-footed ferret reintroduction areas and secure long-range management assurances necessary to perpetuate viable, wild populations?

All ferret reintroductions in the United States have been accomplished under ESA section 10(j) provisions, which relax many of the strict prohibitions of the ESA. Section 10(j) has been an important management tool and was necessary for initial ferret reintroduction efforts. Nevertheless, 10(j) also has limitations and liabilities. Despite successful development of ferret reintroduction projects over most of the best remaining habitats in the United States since 1991, the administrative processes required to establish 10(j) experimental population sites typically require 2 years to complete and considerable investments of staff and funding. It is not a provision that allows rapid response to new opportunities. More importantly, 10(j) is somewhat one-sided in effect and does not provide long-range assurances of support by affected parties. It can hinder implementation of program changes in response to identified needs and has been used by involved agencies to justify positions of social and political expediency rather than to fulfill conservation obligations. Other than reducing political opposition to initial reintroduction efforts, 10(j) has done little to assure reestablishment of ferrets.

Still, we do not advocate stronger regulations or constraints to guide ferret recovery; indeed, we suggest the opposite. The time to be most careful and restrictive with species like the ferret, condor, and red wolf is when they are declining, so as to keep them from slipping into such a precarious abyss in the first place. A process is needed through which responsible agencies are given sufficient resources and broader latitude to quickly develop site-specific strategies that define the boundaries of proposed recovery areas, prescribe the scope of agreements, and, like 10(j), hold no private parties accountable for uses or development of their property that might result in inadvertent losses of endangered ferrets. The ferret program needs to become even more proactive and not shy away from potential risks of individual project failure and animal losses. Again, we need to cast a wide net while reducing the fear of repercussions and impacts to private property that accompany efforts to recover endangered species.

How can resources allocated to endangered species recovery at the national level be better prioritized and distributed to address biological imperatives?

The manner in which endangered species program priorities are established and funded warrants review. Although we certainly support other programs and efforts to recover endangered species, overall national priorities should be biologically based and focused on those species in greatest peril and for which habitat protection would have the greatest overall ecological benefit. Black-footed ferret recovery has achieved some remarkable successes despite a history of inadequate funding. Increased funding could have substantially accelerated species recovery, focused greater attention on critical program elements such as habitat conservation and restoration and expanded partnerships, and perhaps would have helped avoid some of the pitfalls encountered.

Enormous resources have been poured into recovery efforts for the gray wolf and grizzly bear in the Rocky Mountain region with great success and public benefits, but these species enjoy stable habitats over significant portions of their historical ranges—habitats that support large, nonthreatened populations to the north. The black-footed ferret has no comparable safety net of extant population reservoirs. Moreover, the grassland/steppe ecosystem upon which the ferret depends is imminently more threatened, and its loss would have far-reaching consequences to a host of other native plant and wildlife species.

We recognize that these questions and suggestions address larger issues of regulation, policy, and current management direction and practices for numerous State and Federal agencies. We also understand that there are no easy fixes and that change may be slow in coming. Still, what better example of a species recovery program could be used as a springboard to critically review functional elements of ESA, interagency coordination and management needs, partnership capabilities, and administrative processes needed to secure greater habitat stability and foster species recovery? These questions and issues are in need of more focused scrutiny and attention by FWS, partner agencies, organizations, and tribes of the BFFRIT and other endangered species programs.

Acknowledgments

General data on red wolf and California condor used in this paper were obtained from FWS recovery program staff. The interpretation and analyses of those data presented here are our own.

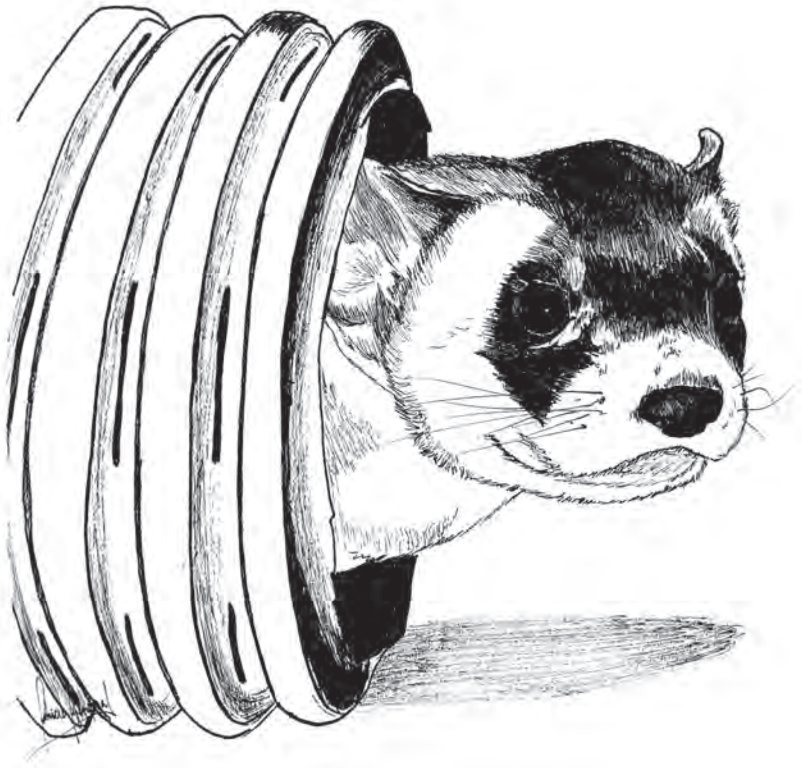
Recovery Plans and Recovery Program Analysis Reports

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management planning workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

Hutchins, M., Wiese, R.J., and Bowdoin, J., 1996, Black-footed ferret recovery program analysis and action plan: Bethesda, Md., American Zoo and Aquarium Association, 137 p.

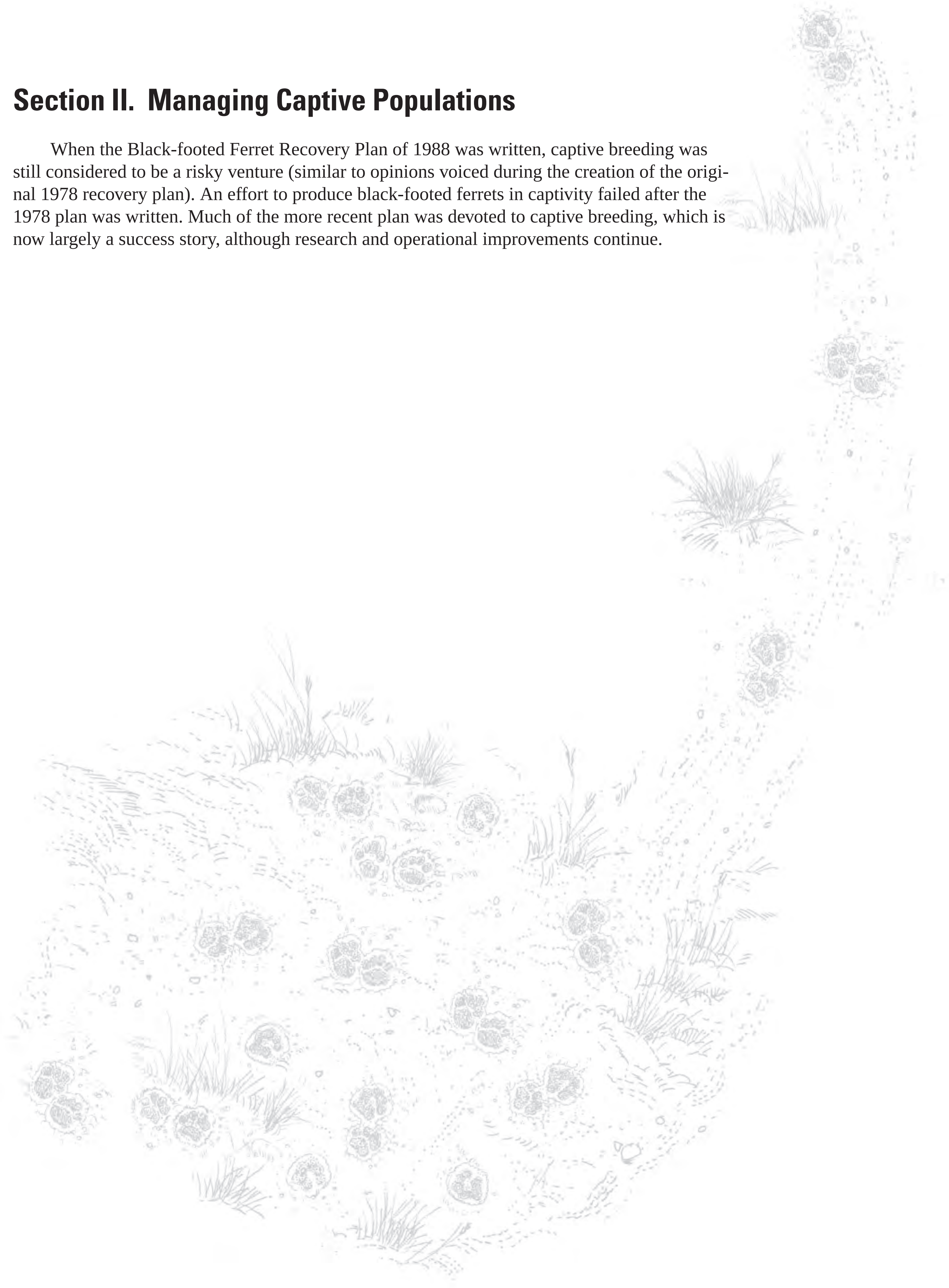
U.S. Fish and Wildlife Service, 1978, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 145 p.

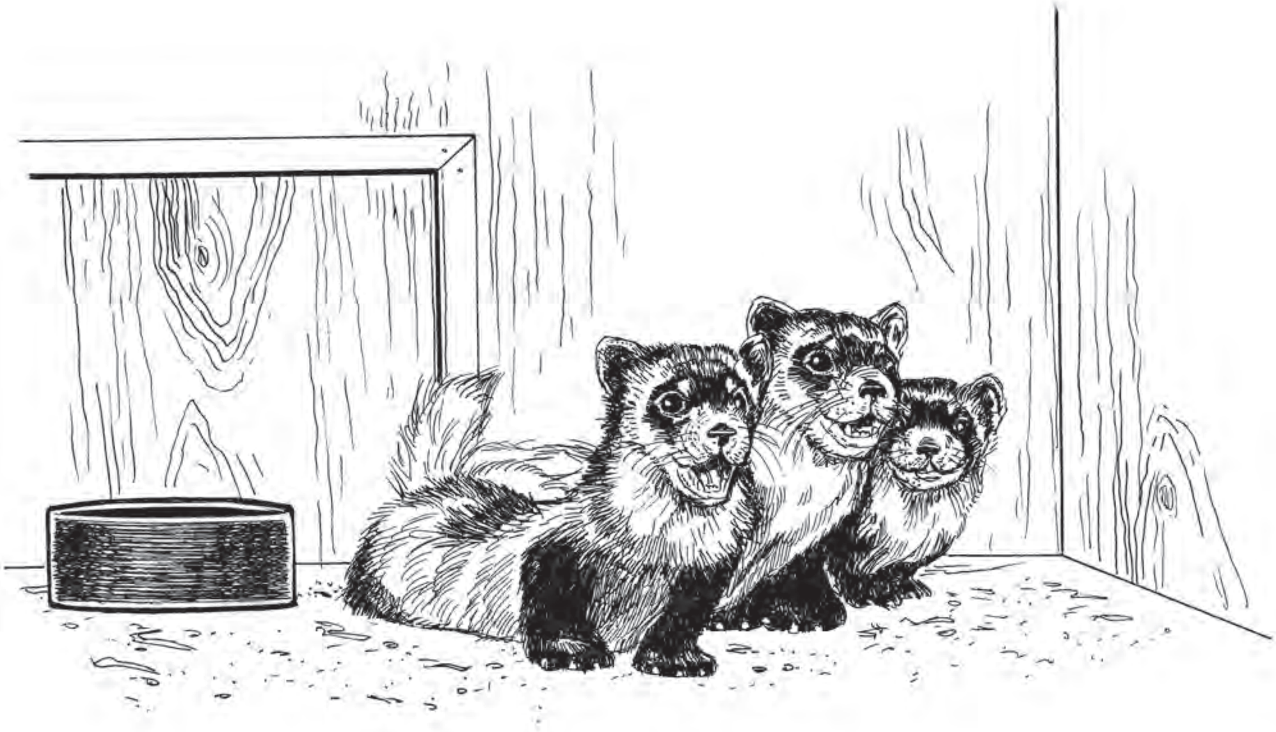
U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.



Section II. Managing Captive Populations

When the Black-footed Ferret Recovery Plan of 1988 was written, captive breeding was still considered to be a risky venture (similar to opinions voiced during the creation of the original 1978 recovery plan). An effort to produce black-footed ferrets in captivity failed after the 1978 plan was written. Much of the more recent plan was devoted to captive breeding, which is now largely a success story, although research and operational improvements continue.





An Adaptive Management Approach for Black-footed Ferrets in Captivity

By Paul E. Marinari[1] and Julie S. Kreeger[1]

Abstract

Management of black-footed ferrets (*Mustela nigripes*) in captivity has historically utilized a flexible, adaptive approach as additional information about the species is obtained. Increased survivorship at reintroduction sites within the ferret's historical range has further allowed innovative approaches to animal husbandry. Ferret recovery has benefited from changes in breeding schemes, nutrition, and vaccinations. Production of kits increased when animals were paired during daytime hours and allowed to remain together for 3 consecutive days. The Toronto Zoo Small Carnivore Diet was found to be a well-balanced, cost-effective, nutritious food for ferret maintenance and reproduction. PureVax® Ferret Distemper Vaccine provided protective titers under a variety of management scenarios. Changing program needs and flexibility in animal management are assessed yearly in order to balance maintenance of genetic diversity with maximum productivity.

Keywords: adaptive management, black-footed ferret, breeding, captive, *Mustela nigripes*, nutrition, reproduction, vaccination

Introduction

Captive management of endangered species requires an adaptive approach, incorporating new information relevant to changing program goals while ensuring quality animal care. Additionally, a system of checks and balances is needed to ensure that changes in management do not adversely affect either animal health or the primary goals of captive breeding—productivity and maintenance of genetic diversity. The fate of the black-footed ferret (*Mustela nigripes*) was placed in the hands of captive breeding efforts in the late 1980s when a decline of the last known wild population was identified. The decline of this population, located near Meeteetse, Wyo., led to the capture of 18 individuals of the species and was the start of a complex, multipartner recovery effort, which is conducted under the auspices of the American Zoo and Aquarium Association's Species Survival Plan® (SSP) program and is guided by the Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) and a manual of husbandry techniques (Lyster and others, 2002).

One of the primary goals identified in the Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) involves development and maintenance of a large, stable, and genetically managed captive breeding population, which has been further defined as a core breeding population of 240 adults (90 males, 150 females) located in six geographically separated facilities. Facilities currently housing captive breeding populations include the U.S. Fish and Wildlife Service's (FWS) National Black-footed Ferret Conservation Center (Center) in Wellington, Colo., (originally managed by the Wyoming Game and Fish Department and later the FWS at Wheatland, Wyo.), the Smithsonian National Zoological Park's Conservation & Research Center (Virginia), the Louisville Zoo (Kentucky), the Cheyenne Mountain Zoo (Colorado), the Toronto Zoo (Ontario, Canada), and the Phoenix Zoo (Arizona).

At the outset of the captive breeding program, all facilities tried to follow identical animal husbandry and management protocols based on the initial success of the Wyoming Game and Fish Department's (WGFD) program. Since 1987, this has led to the production of over 5,100 black-footed ferret kits through natural breeding and assisted reproductive technology. During this time, much has been learned about ferret behavior, reproductive technology, nutrition, and other factors associated with animal husbandry and captive colony maintenance. The ability to experiment with different management schemes in the ferret program has been key to these achievements. In the mid-1990s, the FWS assumed operational oversight of the largest ferret colony, which is located at the Center. The Center houses approximately 55 percent of the world's captive black-footed ferrets and serves as the hub for all ferret-related activities. Given the large population of ferrets housed there, the Center is an ideal place to implement a flexible and adaptive approach in all areas of black-footed ferret captive management. Additionally, the Center staff works both independently and in collaboration with research-

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ers to investigate questions concerning reproduction, nutrition, disease, and genetics as they relate to captive breeding.

Many changes have been incorporated into the captive breeding program based on studies addressing factors that affect the number of kits produced and weaned (defined as kits surviving to 90 days of age). This paper reviews three areas of management that have been addressed through studies at the Center: breeding strategies, nutrition, and vaccination against disease.

Breeding Strategies

A primary goal of the SSP is to optimize genetic management of the captive population (Ballou, 1984; Russell and others, 1994; Miller and others, 1996) by maintaining 80 percent of the genetic diversity present in the founder population for the next 25 years. Since only 7 of the original 18 animals successfully reproduced, genetic diversity has been limited from the outset. Males and females are paired utilizing the mean kinship and inbreeding coefficient strategy (Ballou and Oakleaf, 1989). This strategy identifies several potential males for each female in the SSP breeding population. Efforts to equalize founder representation are succeeding (Wisely, 2001), indicating that the mean kinship and inbreeding coefficient strategy is an appropriate tool for managing the captive population.

Prior to 1996, all ferrets at the Center, as well as those at other captive breeding facilities, were paired by using procedures developed by the WGFD. This involved pairing of animals at night with a high degree of human intervention. Staff at the Louisville Zoo tried a different, less intensive approach to male and female pairings that resulted in very successful kit production. In 1996, Center staff decided to conduct a more extensive study comparing the Wyoming and Louisville methods.

In 1996, the entire ferret colony at the Center was kept under strict quarantine procedures during the breeding season. Access to the animals was limited to immediate staff. Additionally, before coming in contact with any ferrets, all employees showered and changed into clothes that remained onsite. Vehicle traffic near the main breeding building was restricted to emergency use in order to minimize possible disturbance to the ferrets.

Black-footed ferret females were divided between the two breeding schemes being investigated (*n* = 36, Wyoming; *n* = 29, Louisville). Only females aged 1–3 years were included in the study, as these age classes form the core of the captive breeding population. All females were housed in the main breeding building and were treated similarly up to the moment of pairing with their chosen male. Each animal was maintained on a strict diet, known as 60/40, which consisted of a mixture of ground rabbit, commercial mink chow, and various additives, formulated by staff of the WGFD prior to 1996. During the breeding season, rendered lard was added to the 60/40 diet of expectant females only. Two months prior to the breeding season, each ferret was weighed and assigned a target weight that was determined by technicians using visual cues of overall body condition. Amount of food provided to the animals was altered based on weight over a 2-month period. As the breeding season progressed, weekly vulvar measurements were performed and recorded. Vaginal cytology and vulva size were used to monitor reproductive readiness in both groups (Williams and others, 1992). In the Louisville method, males were brought to the females' cages and were not given access to the upper nest box at night. Additionally, once a positive sperm check was obtained, the pair was left together for 3 consecutive days and nights. In the Wyoming method, females were brought to the males' cages, confined to the cage surface (1.2 × 1.2 m), which contained a breeding box, and separated from the males during daylight hours.

Peterson (1996) summarized findings of this study for the FWS's 1996 annual progress report. Fecundity, defined as the proportion of bred females that whelped, was higher with the Louisville method (55 percent versus 36 percent). The average litter size per female bred with the Louisville method was 2.65 ± 2.31 (mean ± SE), which was significantly different from the average litter size for the Wyoming breeding method (1.46 ± 1.82; one-way ANOVA, $P = 0.05$). The average number of kits weaned per whelping female with the Louisville method was 3.13 ± 1.93, which was significantly different from results of the Wyoming method (1.54 ± 1.56; one-way ANOVA, $P = 0.02$).

The higher whelping rate and greater number of kits produced with the Louisville method indicated that this management scheme would be beneficial to overall program goals—maintenance of genetic diversity and production of as many kits as possible. Greater kit production with the Louisville method could be a result of several factors, including less stress because of minimal human interactions while males and females were paired and more time for the animals to copulate, as black-footed ferrets are induced ovulators. Pairs were observed copulating multiple times throughout the day, perhaps providing greater stimuli for ovulation to occur. There is also a cost savings associated with the Louisville method, as additional staff are no longer necessary to monitor pairs at night. Daytime ferret keepers balance activities related to ferret breeding with husbandry chores. The Louisville method has now become standard operating procedure at all captive breeding institutions. At the Center, further refinements have occurred during the past several years to make pairings more efficient. Testicular and vulvar measurements have been discontinued in favor of electroejaculation and vaginal cytology to determine male and female reproductive readiness. Video monitoring has also been discontinued. Sperm checks are now performed opportunistically, and staining (Dip Quick; Jorgensen Laboratories, Inc., Loveland, Colo.) is used to determine the success of pairings.

Nutrition

Black-footed ferrets rely predominantly on prairie dogs (*Cynomys* spp.) for food in the wild (Campbell, 1987). Logistically, it would be extremely difficult to feed all ferrets maintained in the captive breeding program a diet of 100 percent prairie dogs, so alternative diets have been investigated. Initially, captive ferrets were fed a mink chow and rabbit-based diet (the aforementioned 60/40 diet) that included a variety of additives thought to be important for maintaining a healthy breeding population based on information from domestic ferret (*Mustela putorius furo*) and mink (*M. vison*) captive breeding programs. As additional captive breeding facilities were incorporated into the program, feeding strategy guidelines and protocols were relaxed. Several nutritionists were concerned that the 60/40 diet had excessive polyunsaturated fatty acids. Oyarzun and others (1994) analyzed and evaluated common diets used throughout the captive breeding program in the mid-1990s and determined that the 60/40 diet used at the Metro Toronto Zoo (now the Toronto Zoo) greatly exceeded dietary recommendations established for mink as well as nutrient levels reported in the natural diet of black-footed ferrets (Dierenfeld and McGuire, 1989). Oyarzun and others (1994) stated that, even though mineral levels were not high enough to cause acute toxicosis, feeding of higher than recommended levels over an extended period of time might have adverse effects (Lyster and others, 2002). Nutritionists at the Toronto Zoo continued to alter the diet composition so that it more closely fit accepted dietary requirements. This research led to formulation of the horse-based Toronto Zoo Small Carnivore Diet produced by Milliken Meat Products, Ltd., Scarborough, Ontario, Canada.

In 2000, a study was conducted at the Center to compare the two diets (60/40 and Toronto Zoo Small Carnivore) used in the captive breeding program. The primary objective of the study was to examine the effect of the diets on reproductive output. As sample sizes were small (four females and four males in each group), we were looking only for obvious and detrimental deviations from results achieved with the standard 60/40 diet. Larger sample sizes would have provided greater statistical power; however, using additional females in the study might also have reduced our ability to maintain genetic diversity and produce kits for reintroduction. Supplemental vitamin K, believed to decrease the frequency of intra-abdominal hemorrhage (blue-belly) in kits, was provided to bred and nursing females at the same dose and time period for both groups. A less labor-intensive strategy to raise kits was used on all litters at the Center. This strategy not only reduced handling time but also decreased the amount of supplemental diet offered to individual kits. Weights of adults were only monitored during preliminary stages of the study to determine adequate serving sizes and guard against large fluctuations in weight. For females, the number of kits born and those surviving to 50 days of age were examined. Fifty days of age was chosen as a cutoff point for the study because all kits are fed identical diets beginning at that age. The response variable for males was number of sperm per milliliter in ejaculate.

A key advantage to the Toronto Zoo Small Carnivore Diet is that it is made under strict quality control (Canadian Food Inspection Agency). The prepackaged diet was found to be very convenient to use, less labor intensive, and more sanitary than the 60/40 diet produced in-house. The majority of ferrets readily accepted the diet and seemed to prefer it at first feeding. Overall, there was no difference between the two diets in the number of kits born per female (3.5) or the number of kits per female surviving to 50 days of age (3.25). Sperm production appeared to be lower in males fed the Toronto Zoo Small Carnivore Diet, but concentrations were above acceptable limits (250 × 10^6 sperm/mL). Staff at the Center also noticed that kits readily ate the Toronto Zoo Small Carnivore Diet at early stages of development.

Based on these feeding trials in 2000, the Toronto Zoo Small Carnivore Diet was determined to be effective and convenient for use at the Center and replaced the 60/40 diet; however, in 2003 the United States banned import of all meat products from Canada as a result of mad cow disease (bovine spongiform encephalopathy). Accordingly, we investigated alternative diets, including the Dallas Crown Carnivore Diet (Dallas Crown, Inc., Kaufman, Tex.). Earlier feeding trials at the Phoenix Zoo found this diet to be suitable for ferret maintenance and production. The SSP Nutrition Advisory Group also endorsed the diet as an acceptable alternative if the Toronto Zoo Small Carnivore Diet was unavailable. In keeping with our efforts to improve management in the captive breeding program, in 2004 we also evaluated the effect of the Toronto and Dallas Crown diets on sperm production and compared the results to those from black-footed ferrets fed a more natural diet of prairie dogs. There were no significant differences in the response variable among any of the three diets. The Toronto Zoo Small Carnivore Diet is generally preferred by ferret caretakers because of its more even consistency, which makes it easier to feed to ferrets.

Vaccination

Transport of black-footed ferrets across State and international borders may require rabies vaccination, depending on individual State or country regulations. If required, black-footed ferrets over 3 months of age are vaccinated with Imrab® 3 (Merial, Inc., Athens, Ga.). This vaccine is approved for use in domestic ferrets and recommended for yearly revaccination. It is also recommended that ferrets in outdoor pens be vaccinated in areas where rabies is endemic. Rabies vaccination must be by or under the direct supervision of a licensed veterinarian.

Prevention of canine distemper in captive black-footed ferrets has been an important management consideration since the inception of the captive breeding program. Captive ferrets have succumbed to both natural (Williams and others, 1988) and vaccine-induced canine distemper virus (CDV) infections (Carpenter and others, 1976). The search for a safe and effective canine distemper vaccine for use in captive and free-ranging black-footed ferret populations has been a priority for ferret recovery (Wimsatt and others, this volume).

Historically, ferrets in the captive breeding program were vaccinated against CDV with an inactivated virus plus adjuvant. The vaccine was prepared yearly by Dr. M.J.G. Appel of Cornell University. Adjuvant was prepared separately. This vaccine was used until 2002, but no data on duration of immunity and protection against CDV were collected. The recent availability of a commercial, monovalent, canary pox-vectored vaccine for use in domestic ferrets, PureVax® Ferret Distemper Vaccine (Merial, Inc., Athens, Ga.), provided a new possibility for vaccination of captive black-footed ferrets. The vaccine had been tested in the Siberian polecat (*Mustela eversmannii*), a species closely related to the black-footed ferret, with promising results (Wimsatt and others, 2003).

Since management of young black-footed ferrets varies according to their ultimate fate (i.e., release to the wild or captive breeding), we examined several different paradigms of vaccination and the resultant serum neutralization titers. Vaccine used in these studies was a generous donation from Merial. The Wyoming State Veterinary Laboratory in Laramie performed serum neutralization titers.

Three groups of young of the year black-footed ferrets were used. Group 1 consisted of 13 ferrets from multiple litters. These animals were vaccinated intramuscularly with PureVax Ferret Distemper Vaccine. Vaccinations were administered in the right thigh at approximately 60, 74, and 88 days of age. Blood for titers was drawn from the external jugular vein of anesthetized ferrets every 2 weeks, coinciding with vaccinations to minimize handling of young animals. Final blood samples were drawn 2 weeks after the last vaccination. Group 2 included 12 ferrets subjected to vaccination and blood sampling protocols identical to those for group 1, except the PureVax vaccine was given subcutaneously. Group 3 consisted of nine animals subjected to a protocol chosen to approximate the preconditioning of young ferrets for release to the wild. Young preconditioned ferrets are placed in outdoor pens at an early age and often not recaptured for months. Ferrets in this group were vaccinated subcutaneously at 60 days of age and again at 120 days of age. Blood samples were taken at initial vaccination and at 74, 120, and 134 days.

Serum neutralization titers of >1:128 are considered protective (E. Williams, oral commun., 1999). Prior to vaccination, all groups had median titers of <1:8. All ferrets developed protective titers of >1:128 following the second vaccination. Subsequent vaccinations resulted in increased titers. Ten of the ferrets that received intramuscular injections of PureVax were tested 1 year postvaccination, and eight (80 percent) had protective titers.

Results of these studies indicate that black-footed ferrets vaccinated with a minimum of two doses of PureVax Ferret Distemper Vaccine developed protective titers. Three doses of vaccine resulted in increased titers and provided 80 percent of vaccinated ferrets with protective titers up to 1 year later. Based on these results, captive breeding facilities are now encouraged to administer a minimum of two canine distemper vaccinations in young ferrets, beginning at the age of 60 days.

Conclusions

It is apparent that black-footed ferret captive breeding facilities benefit from a flexible management approach. The ability of the program to use adaptive techniques in all areas of ferret management is inextricably linked to the success of reintroduction activities. A stable captive breeding population and an increased number of reintroduction sites have allowed facilities to be more creative in their management decisions. Changes in the program are acceptable only if they do not have a detrimental effect in terms of overall production of animals. Production of kits has been consistent over time, and weaning success continues to improve. Many other changes have been made throughout the history of captive management, including the use of ALPHA-dri™ bedding material (Shepherd Specialty Papers, Watertown, Tenn.), elimination of additional vitamin K supplement, and less labor-intensive dietary management of kits. We will continue to assess our methods on an annual basis and adapt our management in order to provide a stable source of animals to meet the ever-changing needs of the black-footed ferret recovery program.

References Cited

Ballou, J.D., 1984, Strategies for maintaining genetic diversity in captive populations through reproductive technology: Zoo Biology, v. 3, p. 311–323.

Ballou, J.D., and Oakleaf, R., 1989, Demographic and genetic captive-breeding recommendations for black-footed ferrets, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 247–267.

Campbell, T.M., 1987, Food habits of Wyoming black-footed ferrets: American Midland Naturalist, v. 117, p. 208–210.

Carpenter, J.W., Appel, M.J.G., Erickson, R.C., and Novilla, M.N., 1976, Fatal vaccine-induced canine distemper virus infection in black-footed ferrets: Journal of the American Veterinary Medical Association, v. 169, p. 961–964.

Dierenfeld, E.S., and McGuire, J.T., 1989, Seasonal variation in prairie dog carcass composition: New York Zoological Society, 33 p.

Lyster, J., Lockhart, M., Marinari, P., and Garelle, D., eds., 2002, Black-footed ferret husbandry manual: Unpublished report available from the National Black-footed Ferret Conservation Center, 118 p.

Miller, B., Reading, R.P., and Forrest, S., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Oyarzun, S.E., Self, K., Valdes, E.V., Carnio, J.S., Shamir, A.B., Wrobel, M., and Musson, A., 1994, Black-footed ferret SSP 1994 nutrition report for the Metro Toronto Zoo: Toronto, Metro Toronto Zoo, 20 p.

Peterson, D., 1996, A comparison of black-footed ferret (*Mustela nigripes*) productivity under different captive management regimes: Laramie, Wyo., U.S. Fish and Wildlife Service, 26 p.

Russell, W.C., Thorne, E.T., Oakleaf, R., and Ballou, J.D., 1994, The genetic basis of black-footed ferret reintroduction: Conservation Biology, v. 8, p. 263–266.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

Williams, E.S., Thorne, E.T., Appel, M.J.G., and Belitsky, D.W., 1988, Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming: Journal of Wildlife Diseases, v. 24, p. 385–398.

Williams, E.S., Thorne, E.T., Kwiatkowski, D.R., Lutz, K., and Anderson, S.L., 1992, Comparative vaginal cytology of the estrous cycle of black-footed ferrets (*Mustela nigripes*), Siberian polecats (*M. eversmanni*), and domestic ferrets (*M. putorius furo*): Journal of Veterinary Diagnostic Investigation, v. 4, p. 38–44.

Wimsatt, J., Biggins, D., Innes, K., Taylor, B., and Garell, D., 2003, Evaluation of oral and subcutaneous delivery of an experimental canarypox recombinant canine distemper vaccine in the Siberian polecat (*Mustela eversmanni*): Journal of Zoo and Wildlife Medicine, v. 34, p. 25–35.

Wisely, S.M., 2001, Conservation biology of the black-footed ferret (*Mustela nigripes*)—changes in genetic diversity and morphology before, during and after a population bottleneck: Laramie, University of Wyoming, Ph.D. dissertation, 94 p.

Use of Reproductive Technology for Black-footed Ferret Recovery

By JoGayle Howard,[1] Rachel M. Santymire,[1] Paul E. Marinari,[2] Julie S. Kreeger,[2] Linwood Williamson,[1] and David E. Wildt[1]

Abstract

Assisted reproductive techniques such as artificial insemination (AI), in vitro fertilization, and sperm cryopreservation have been postulated to be "high-tech" strategies for saving endangered species from extinction; however, there has been limited application of assisted breeding in wildlife management. This report illustrates how reproductive technology has been utilized in an integrated conservation program to save the endangered black-footed ferret (*Mustela nigripes*). Considered extinct until a remnant population was discovered in Wyoming in 1981, the last remaining 18 black-footed ferrets were captured to establish a captive breeding program. In 1988, the U.S. Fish and Wildlife Service developed a Black-footed Ferret Recovery Plan, which emphasized species preservation through natural breeding, development of assisted reproductive technology, and establishment of multiple reintroduction sites, among others. A multi-institutional propagation program has been highly successful. Approximately 250 animals currently reside in six breeding facilities, and >500 black-footed ferrets survive in the wild from reintroduced animals. Methods for semen collection, AI, and sperm cryopreservation were developed first in domesticated ferrets (*Mustela putorius furo*) and the closely related Siberian polecat (*Mustela eversmannii*) and now are used routinely in black-footed ferret management to (1) assess sperm status prior to natural breeding; (2) circumvent cases of sexual incompatibility; (3) enhance reproduction in nonbreeding individuals to retain existing genetic diversity; (4) increase founder representation; (5) establish a genome resource bank to preserve valuable germ plasm; and (6) produce additional offspring for reintroduction. To date, 128 black-footed ferret kits have been produced by AI using fresh or frozen semen. The black-footed ferret represents a model for reproductive biotechniques contributing to a multidisciplinary species recovery and reintroduction program.

Keywords: artificial insemination, assisted reproduction, genetic management, genome resource banking, semen

Introduction

The value of reproductive technologies to ex situ and in situ wildlife management in helping conserve genetic and biological diversity has been considered for years. Assisted reproductive technologies such as artificial insemination (AI), in vitro fertilization (IVF), embryo transfer, and gamete/embryo cryopreservation offer many advantages for managing small populations, largely by ensuring that all genetically valuable animals reproduce (Ballou, 1984; Howard, 1993, 1999; Wildt and Roth, 1997; Wildt and others, 1997). The potential of assisted reproduction could be enhanced further by developing genome resource banks (repositories of cryopreserved sperm, eggs, and embryos), thus preserving valuable genetic material for future generations. The combined use of assisted breeding and germ plasm banks also has potential for infusing genetic material from wild-born individuals into genetically stagnant ex situ populations or even for exchanging genetic material between isolated wild populations (Holt and others, 1996; Wildt and others, 1997).

Despite these advantages, assisted reproduction has not been used consistently in practical wildlife management and conservation, largely for one reason. Until recently, no wildlife species had been sufficiently studied that its reproductive biology was so comprehensively understood that assisted breeding could become routine. It commonly is assumed that reproductive knowledge and techniques established for laboratory rodents, domestic farm species, and even humans are readily adaptable to propagating or overcoming infertility in wild animals (Wildt and others, 2001a,b). This is a misperception because all species have naturally evolved, unique, species-specific reproductive mechanisms, most of which have not yet been elucidated. Without such specific information, no assisted breeding technique can ever become routine.

There still is a need to demonstrate how such reproductive strategies can be used pragmatically. In this paper, we demonstrate how management and conservation of an endangered carnivore, the black-footed ferret (*Mustela nigripes*), have benefited from the application of the reproduc-

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tive sciences, including assisted breeding. We assert that the lessons learned from (1) working in partnership with wildlife managers and ex situ breeding institutions, (2) taking a systematic basic and multidisciplinary research approach, and (3) integrating knowledge have helped to recover and reintroduce this endangered species into nature.

Black-footed Ferret Recovery

Between the fall of 1985 and spring of 1987, the Wyoming Game and Fish Department, in cooperation with the U.S. Fish and Wildlife Service, captured the last 18 free-ranging black-footed ferrets from Meeteetse, Wyo., a location known to have sylvatic plague and canine distemper (Forrest and others, 1988; Williams and others, 1988; Thorne and Oakleaf, 1991). In the spring of 1987, captive breeding was successful, and two litters of black-footed ferret kits were born. Given the species' critical status, a recovery plan for ex situ propagation and reintroduction was a high priority. A workshop was held in 1986, facilitated by the Conservation Breeding Specialist Group (CBSG) of the Species Survival Commission of the World Conservation Union (International Union for the Conservation of Nature and Natural Resources). Widespread stakeholder participation was emphasized, and the workshop was attended by representatives from State and Federal wildlife and land management agencies as well as experts in mustelids, small population biology, reproduction, nutrition, veterinary medicine, and genetics. Using workshop information (Seal and others, 1989), the U.S. Fish and Wildlife Service developed an official Black-footed Ferret Recovery Plan in 1988 (U.S. Fish and Wildlife Service, 1988) that emphasized species preservation through research, a multi-institutional ex situ propagation program, and establishment of multiple reintroduction sites. The goal of the ex situ breeding program was to maintain ~240 ferrets (90 males, 150 females) in captivity but in multiple institutions to avoid a catastrophe that might affect any single facility. The aim of the eventual reintroduction program was to establish a total of 1,500 ferrets in at least 10 self-sustaining, free-ranging populations by the year 2010. The wild populations, scattered geographically within the ferret's former range, each were to be composed of at least 30 breeding adults.

Throughout discussions of the ex situ and (eventually) in situ metapopulation structure, the role of sound scientific research, including the potential of reproductive technologies, was always recognized. Managers were especially keen to determine whether such techniques could be useful for evaluating fertility and for developing AI with fresh or cryopreserved spermatozoa, all for the purpose of supporting ex situ breeding and especially avoiding further losses in genetic diversity. One early concept was to establish a black-footed ferret genome resource bank, a frozen repository of spermatozoa from the most genetically valuable males, especially those that failed to reproduce by natural breeding.

Ex Situ Natural Breeding

Intensive management by the Wyoming Game and Fish Department resulted in production of offspring in 1987 and all subsequent years, which allowed dividing the ex situ population into six subcolonies at zoological institutions in North America. The U.S. Fish and Wildlife Service assumed the responsibility of managing the Wyoming breeding facility in 1996 and renamed it the National Black-footed Ferret Conservation Center. Since 1987, the multi-institutional ex situ breeding program has produced >5,100 ferrets (Marinari and Kreeger, this volume) while generating extensive knowledge on ferret biology.

For the past decade, the cooperative effort among the breeding facilities has been guided by the Black-footed Ferret Species Survival Plan® (SSP), a population management strategy of the American Zoo and Aquarium Association designed to maintain a self-sustaining ex situ population while providing animals for reintroduction. Breeding recommendations also are provided in an attempt to equalize genetic representation of the few original wild-born founders. SSP managers determine specific pairs for breeding on the basis of a mean kinship value, a measure of how related an individual is to the remaining population (Ballou and Lacy, 1995; Wisely, this volume). Demographic data, including reproductive lifespan, fecundity, age distribution, and sex ratio, are considered in predicting population stability and growth rate over time. Currently, there are ~250 black-footed ferrets maintained in the SSP program at six locations.

Reintroduction

The ability to produce ferrets in captivity allowed reintroduction to begin in 1991, initially into the Shirley Basin of southeastern Wyoming (Miller and others, 1993; Biggins and others, 1997). A few animals survived over winter, and additional ferrets were released at the same site in subsequent years. In 1995, reintroduction efforts were suspended in Wyoming because of a sylvatic plague outbreak and the loss of vital prairie dog (*Cynomys* spp.) colonies on which the ferrets depend for food and shelter. Subsequent ferret reintroduction sites were established in Conata Basin in South Dakota (Badlands National Park and Buffalo Gap National Grassland in 1994) and Montana (Charles M. Russell National Wildlife Refuge in 1994; Fort Belknap Indian Reservation in 1996). Arizona became the fourth State in the reintroduction program in 1996 with ferret releases in Aubrey Valley. Utah was added as the fifth State in 1999 when ferrets were released in Coyote Basin near the Colorado border. In the fall of 2000, the Cheyenne River tribal lands in South Dakota received ferrets. After extensive planning, a site near Janos, Chihuahua, Mexico, received releases in 2001. Successful reproduction and offspring produced in the wild from released ferrets have been documented at all release sites. Survival of released ferrets has improved because of preconditioning, the exposure of ferrets to large outdoor pens with prairie dog burrow systems and live prey prior to reintroduction. Although success varies, the highest survival has occurred at Conata Basin (South Dakota), with >70 percent of captive-born kits and >90 percent of identified wild-born kits surviving over winter and through spring (T. Livieri, oral commun., 2005). As of fall 2005, the wild population was ~500 black-footed ferrets (T. Livieri, oral commun., 2005).

Development of Reproductive Technologies in Animal Models

Potential benefits of reproductive technologies were recognized from the onset of the recovery program. The recovery plan of 1988 (U.S. Fish and Wildlife Service, 1988), the original and official guide for species rescue, encouraged development of methods for reproductive assessment and assisted breeding. It was realized that AI with fresh or frozen spermatozoa could help retain genetic diversity by ensuring reproduction in every valuable individual that failed to breed naturally. Additionally, a genome resource bank containing cryopreserved spermatozoa could preserve extant genes for the future, as well as assist in the genetic management of this small population.

The National Zoological Park's Conservation & Research Center was invited to take a lead role in studying ferret reproductive biology as well as to participate in the ex situ breeding program. We began our reproductive investigations by using the domestic ferret (*Mustela putorius furo*) and the closely related Siberian polecat (*Mustela eversmannii*) as animal models, first to understand general ferret biology and then to use that knowledge for developing assisted breeding (Wildt and others, 1986). Molecular analyses revealed that the domestic ferret, the Siberian polecat, and the black-footed ferret are taxonomically related (O'Brien and others, 1989). All of these species are seasonal breeders with reproductive activity stimulated by long-day photoperiod (Hillman and Carpenter, 1983; Miller and others, 1988; Mead and others, 1990; Miller and Anderson, 1990; Carvalho and others, 1991). Testis size gradually increases beginning in January or February, peaks from March through June and then gradually declines (Neal and others, 1977). The female's breeding season is monoestrus and restricted to the months of March to June, and is characterized by changes in vaginal cytology and an increase in vulvar size. Finally, these species are classified as induced ovulators, with ovulation occurring ~30 hours after a single copulation or an injection of human chorionic gonadotrophin (hCG) or luteinizing hormone (LH) (Mead and others, 1988).

Extensive studies were conducted on domestic ferrets to develop a reliable approach for collecting, processing, and analyzing fresh or cryopreserved spermatozoa (Curry and others, 1989; Wildt and others, 1989; Howard and others, 1991; Van der Horst and others, 1991). More than 300 electroejaculates from nine males were collected to address the (1) effect of temporal spermatogenesis patterns on sperm viability; (2) comparative effectiveness of vaginal versus uterine insemination via an atraumatic laparoscopic approach; (3) influence of sperm number, dilution medium, and time of hCG administration on pregnancy success, gestation interval, and number of offspring produced; and (4) influence of cryodiluent, freezing method, and thawing temperature on the biological competence of frozen-thawed ferret spermatozoa (Wildt and others, 1989; Howard and others, 1991; Howard, 1999). Such basic studies were crucial to developing reliable assisted breeding techniques. An effective electroejaculation protocol was developed in the domestic ferret to consistently collect high-quality spermatozoa from anesthetized males (table 1). Vaginal insemination was determined to be ineffective for producing offspring; none of 10 females became pregnant after spermatozoa were deposited intravaginally (Wildt and others, 1989). In contrast, transabdominal-intrauterine sperm deposition via laparoscopy resulted in high pregnancy success. Seventeen of 24 ferrets (70.8 percent) inseminated in this fashion became pregnant and delivered live young (Wildt and others, 1989). In addition, embryo transfer was developed in the domestic ferret to nonsurgically transfer preimplantation embryos (Wildt and Goodrowe, 1989; Kidder and others, 1999). Comparative assessments of 12 cryopreservation methods determined that a combination of an egg-yolk/lactose cryodiluent, the pellet freezing method, and a 37°C thawing temperature was effective for freeze-thawing ferret sperm and recovering maximal motility and acrosomal integrity.When this cryomethod was

Table 1. Mean (± SE) ejaculate traits, sperm morphology, and acrosomal integrity in the domestic ferret (*Mustela putorius furo*), Siberian polecat (*M. eversmannii*), and black-footed ferret (*M. nigripes*).

	Domestic ferret (*n* = 4 males)[a]	**Siberian polecat (*n* = 8 males)[b]**	**Black-footed ferret (*n* = 97 males)[b]**
Sperm motility (%)	80.7 ± 1.0^c	80.6 ± 2.9^c	51.2 ± 1.8^d
Sperm progression (0–5; 5 = best)	3.3 ± 0.1	3.0 ± 0.2	2.5 ± 0.1
Normal sperm (%)	67.3 ± 1.3^c	74.5 ± 2.6^c	21.0 ± 1.5^d
Normal intact acrosome (%)	92.4 ± 0.5^c	96.8 ± 1.0^c	67.2 ± 2.8^d

[a] Data based on 52 ejaculates from four males (Howard and others, 1991).

[b] Data based on one ejaculate per male (Howard and others, 1996; J. Howard, unpub. data, 1996).

[c,d] Within rows, values with different superscripts are different ($P < 0.05$).

used, 7 of 10 females (70.0 percent) inseminated in utero with frozen-thawed ferret spermatozoa became pregnant (Howard and others, 1991). Overall, reproductive efficiency was high (70.6 percent) after laparoscopic intrauterine AI with fresh or frozen semen (table 2).

The strategy developed for the domestic ferret was subsequently applied to the Siberian polecat and finally to the black-footed ferret. Although sperm motility traits were similar among the three species, there were significantly fewer structurally normal spermatozoa in the black-footed ferret compared to the domestic ferret and polecat (table 1; Howard and others, 1991, 1996). After cryopreservation and thawing, sperm motility and membrane integrity also were less in the black-footed ferret compared to the other species (Howard and others, 1991, 1996). These differences in sperm viability were assumed to be related to the restricted founder base and reduced genetic variation in the black-footed ferret. Nevertheless, the laparoscopic intrauterine AI technique, developed in the domestic ferret, proved effective in its close relatives. Eight of 10 (80.0 percent) Siberian polecats inseminated with fresh or cryopreserved semen became pregnant (table 2), and this high rate provided the confidence to apply the procedure to the rarer black-footed ferret. Four of six (66.7 percent) black-footed ferrets inseminated with fresh or frozen-thawed semen became pregnant and delivered live young (table 2) (Howard and others, 1996; Howard, 1999).

Table 2. Comparison of laparoscopic intrauterine artificial insemination with fresh or frozen-thawed spermatozoa in closely related ferret species. Data from Wildt and others (1989), Howard and others (1991, 1996), and Howard (1999).

	Domestic ferret (*Mustela putorius furo*)	**Siberian polecat (*Mustela eversmannii*)**	**Black-footed ferret (*Mustela nigripes*)**
Number of females inseminated	34	10	6
Number of pregnant females	24	8	4
Pregnancy rate (%)	70.6	80.0	66.7
Number of kits born	116	42	9
Mean (± SE) number of kits/litter	4.8 ± 0.8	5.2 ± 1.0	2.3 ± 0.6

Assisted Breeding to Enhance Reproduction in Black-footed Ferrets

It soon was realized that the reintroduction goal (1,500 breeding ferrets in 10 free-ranging populations by the year 2010) was not achievable at the current rate of propagation in the ex situ natural breeding program. Early experiences revealed that some animals consistently failed to reproduce. Analysis of breeding records indicated that most females (>90 percent) demonstrated a spring estrus on the basis of vaginal cytology changes (markedly increased numbers of superficial, cornified squamous epithelial cells; fig. 1) (Williams and others, 1992; Brown, 1997); however, there was a high incidence (~40 percent) of pseudopregnancy wherein matings were observed (via video camera) and ovulation was confirmed (by an abrupt decrease in superficial cornified cells), but no pregnancy occurred (Williams and others, 1991). Fecal oestradiol and progestogen metabolite profiles in pregnant versus pseudopregnant females were similar (fig. 1; Brown, 1997), suggesting that endocrine dysfunction was not contributing to the problem.

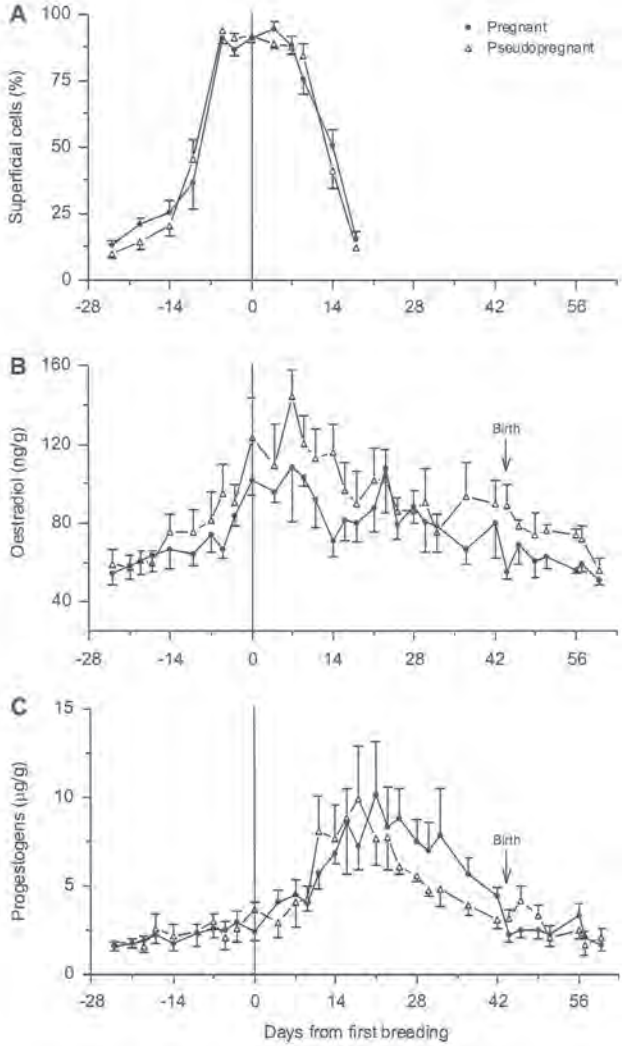

Figure 1. Mean (± SE) percent superficial cells in vaginal lavages (A) and fecal oestradiol (B) and progestogen (C) metabolite concentrations in pregnant (n = 7) and pseudopregnant (n = 9) black-footed ferrets (*Mustela nigripes*). Day 0 is the time of first mating. (From Brown, 1997. Reprinted with permission of the *Journal of Wildlife Management*.)

Interestingly, records analysis indicated that a remarkably high proportion (>50 percent) of prime breeding-age males (1–3 years old) inexplicably failed to sire offspring in captive breeding situations. In 1995, there were 40 such adult males (54.8 percent of the breeding-age male population) that were exposed to prime age, estrual females and yet did not produce young. Simultaneous evaluations also revealed a genetic problem, largely that one of the original wild-born ferret founders was poorly represented in the modern population. This underrepresented lineage had only 43 descendants compared to more than 300 descendants from each of the remaining founder lineages. To help preserve original gene diversity, it was imperative to balance founder representation. This situation was confounded by another challenge in the underrepresented lineage—these males were consistently sexually incompatible with designated mates, largely because of aggression. Together, these issues prompted an examination of the value of reproductive technology and assisted breeding.

At the request of black-footed ferret managers, we agreed to (1) assess reproductive traits and breeding behavior in males with proven versus unproven fertility; (2) establish a genome resource bank containing cryopreserved spermatozoa from the most genetically valuable males; and (3) use AI for improving reproductive efficiency in nonbreeders, all for the ultimate purpose of increasing the number of kits for reintroduction. A survey was conducted in 1996 and 1997 to determine the precise number of prime breeding-age males not siring offspring and the reasons for failed reproduction. As in 1995, a high percentage of 1- to 3-year-old males did not sire young in 1996 (38 of 69 males, 55.1 percent) or 1997 (35 of 60 males, 58.3 percent) (Wolf and others, 2000b). Semen evaluations determined that there were no differences in sperm concentration, motility, or morphology between proven and unproven breeders (Wolf and others, 2000b). A detailed review of breeding data revealed that males failed to reproduce because of improper breeding position, behavioral incompatibility (e.g., aggression), and poor testes development (Wolf and others, 2000b). As much of the problem was behaviorally based, we speculated that assisted reproduction could be beneficial for improving reproductive efficiency.

A systematic strategy was used to establish the genome resource bank. Using the computer software program (SPARKS; International Species Information System, Eagan, Minn.) developed for SSP programs, sperm donors could be selected on the basis of founder representation and mean kinship (Ballou and Lacy, 1995; Johnston and Lacy, 1995; Wisely, this volume). High-priority black-footed ferret males were selected for inclusion in the bank, with semen samples collected and cryopreserved for AI (as part of routine management) or for long-term storage (as a hedge repository of valuable genes).

At the National Zoological Park's Conservation & Research Center, the natural breeding program for black-footed ferrets was modified to include AI. The goals were to (1) produce offspring from behaviorally incompatible animals, especially nonbreeding males, to meet reintroduction demands and (2) increase founder representation in the underrepresented lineage. In achieving these goals, other opportunities arose, including examining the impact of male age on reproductive success. From 1996 through 2003, nonbreeding males of high genetic value were chosen as candidates for assisted reproduction. Overall, 66 females were monitored for natural estrus and were administered hCG or LH (to induce ovulation) 5 to 7 days after maximal vulvar swelling and >90 percent superficial cornified vaginal cells. Twelve to 20 hours later, each female was anesthetized and, under laparoscopic observation, inseminated in utero with fresh or frozen-thawed spermatozoa. Five of six (83.3 percent) females inseminated with semen from founder descendants became pregnant and produced 16 kits (table 3). Males were determined to produce excellent quality semen through 5 years of age, 2 years longer than the normal female reproductive life span (Wolf and others, 2000a). Eight of 11 (72.7 percent) females inseminated with semen from 5-year-old males produced 17 kits (table 3). A total of 28 of 49 (57.1 percent) females gave birth to 95 kits following AI with semen from genetically valuable, nonbreeding males (table 3). Overall, AI resulted in 128 additional black-footed ferret kits, offspring that never would have been born from natural mating.

There were other by-products as well. For example, we observed that a high proportion of 1-year-old males produced aspermic (no sperm) ejaculates during the breeding season (Howard and others, 1998). These males experienced increases in seasonal testicular tumescence (albeit somewhat slower than elders; fig. 2) and copulated with females; however, systematic seminal evaluations revealed that these yearlings produced spermic ejaculates at least 4 weeks later in the breeding season than older counterparts (fig. 2). This asynchrony in sperm

Table 3. Use of laparoscopic artificial insemination to enhance propagation in nonbreeding founder descendants, 5-year-old males, and genetically valuable male black-footed ferrets (*Mustela nigripes*) from 1996 through 2003.

	Founder descendants[a] **(*n* = 3 males)**	**5-year-old males**[b] **(*n* = 5 males)**	**Genetically valuable males**[c] **(*n* = 27 males)**
Number of females inseminated	6	11	49
Number of pregnant females (%)	5 (83.3)	8 (72.7)	28 (57.1)
Number of kits born	16	17	95

[a] Males were descendants of a wild-caught founder whose genetic lineage was underrepresented in the ex situ population.

[b] Reproductive competence was assessed in 5-year-old males.

[c] Despite numerous breeding opportunities, reproductive failure in these genetically valuable males was due primarily to behavioral incompatibility (aggression or shyness) or inappropriate breeding position.

production probably influenced the incidence of pseudopregnancy because aspermic males can induce ovulation following copulation. This was an important observation with significant implications for routine ferret management. Until this finding, males used for breeding were selected on the basis of enlarged testis size. Now, only males with spermic electroejaculates are allowed access to females for natural breeding, and introducing this simple semen assessment technique to the management protocol in 1998 resulted in a striking 20 percent increase in pregnancy success and 59 additional kits available for reintroduction (table 4).

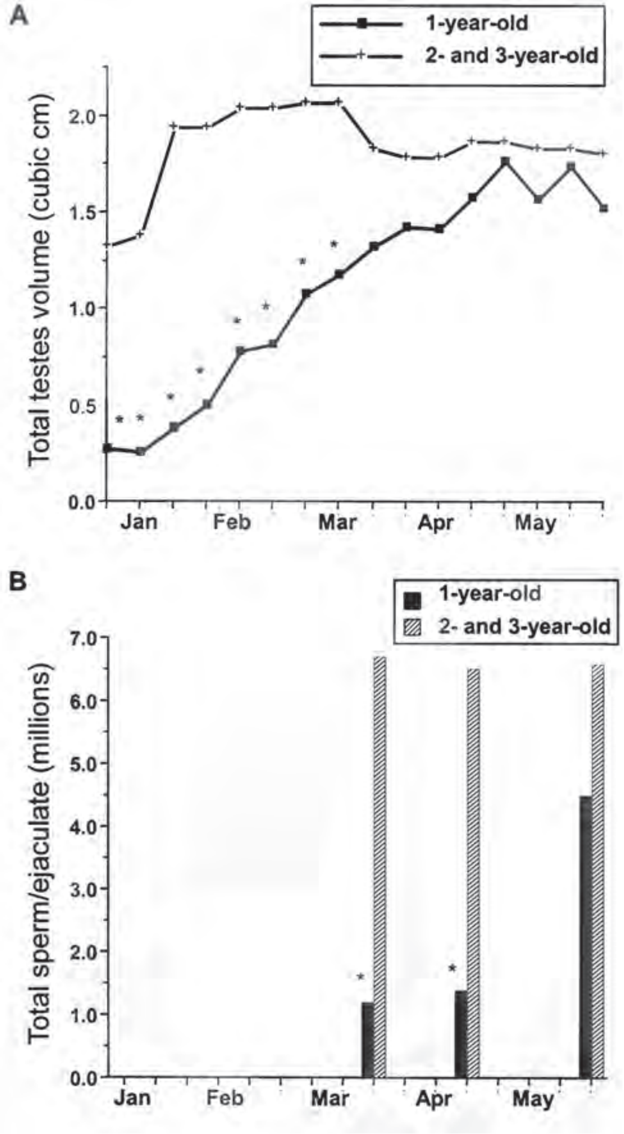

Figure 2. Influence of age on testes development (A) and total sperm/ejaculate (B) in 1-year-old versus 2- and 3-year-old male black-footed ferrets (*Mustela nigripes*). Asterisks indicate differences ($P < 0.05$) between age groups within a month.

Table 4. Propagation in the black-footed ferret (*Mustela nigripes*) using enlarged testes versus spermic ejaculate as the criterion for selecting males for natural breeding.

	Enlarged testes	**Spermic ejaculate**
Number of females bred	84	86
Number of litters	50	69
Pregnancy success (%)	59.5	80.2
Number of kits born	190	249

Priorities for the Future

The black-footed ferret is a provocative example of how reproductive technologies integrated with both ex situ and in situ management plans can benefit species conservation. The positive results are evidence that reproductive techniques are valuable for (1) generating new knowledge of relevance to natural and assisted breeding and (2) producing living, genetically valuable offspring useful for breeding stock and/or reintroduction. Priorities for this species extend far beyond reproductive biology; adequate survival after reintroduction continues to be essential to the black-footed ferret's future. Urban sprawl, sylvatic plague, and poisoning of prairie dogs appear to be never-ending, severe threats. Today, only 2 percent remains of the ~100 million acres of the original prairie dog ecosystem of the Great Plains (Miller and others, 1996). Monitoring for presence of sylvatic plague as well as canine distemper is essential for long-term protection of both prairie dogs and ferrets. Research into the development and use of a sylvatic plague vaccine is ongoing (Rocke, this volume). Even when a vaccine becomes available, there will be enormous distribution challenges. Also, persistent poisoning campaigns and recreational shooting continue to contribute to the collapse of the prairie dog ecosystem.

Finally, a high priority will continue to be education programs, which play a crucial role in public awareness of black-footed ferret conservation issues. Currently, over 30 zoos and wildlife agencies sponsor educational exhibits, often using "ambassador" black-footed ferrets. Gaining public support, especially from landowners who consider prairie dogs pests, is critical to reintroduction success. Many landowners continue to have serious concerns about endangered species, especially perceived governmental interference and restrictions on land use (Reading and Kellert, 1993; Miller and others, 1996). A key factor facilitating landowner support for ferrets has been the designation of the reintroduced population as experimental and nonessential under the Endangered Species Act (see Lockhart and others, this volume, for additional information). Although resulting in a lower level of protection for released ferrets, this strategy has gained local rancher and farmer cooperation while providing some assurance that reintroduced ferrets and traditional land uses can be compatible.

Conclusion

It is apparent that reproductive sciences can play a vital role in a holistic, integrated conservation program to save an endangered species. The contemporary story of the black-footed ferret illustrates the potential for species recovery and reintroduction based on partnerships and multidisciplinary, sound science. Perhaps most important has been the cooperative feature, collaboration among over 30 organizations, including State and Federal agencies, conservation groups, and zoos, that worked together to return ferrets to their former grassland habitats of the Great Plains. Reproductive technologies, including AI and a genome resource bank, have been integrated successfully into the black-footed ferret recovery program to maintain genetic diversity, enhance reproductive efficiency, and produce additional animals for reintroduction.

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References Cited

Ballou, J.D., 1984, Strategies for maintaining genetic diversity in captive populations through reproductive technology: Zoo Biology, v. 3, p. 311–323.

Ballou, J.D., and Lacy, R.C., 1995, Identifying genetically important individuals for management of genetic diversity in pedigreed populations, *in* Ballou, J.D., Gilpin, M., and Foose T.G., eds., Population management for survival and recovery: New York, Columbia University Press, p. 76–111.

Biggins, D.E., Miller, B.J., Clark, T.W., and Reading, R.P., 1997, Conservation management case studies—the black-footed ferret, *in* Meffe, G.K., and Carroll, C.R., eds., Principles of conservation biology: Sunderland, Mass., Sinauer Associates, p. 420–426.

Brown, J.L., 1997, Fecal steroid profiles in black-footed ferrets exposed to natural photoperiod: Journal of Wildlife Management, v. 61, p. 1428–1436.

Carvalho, C.F., Howard, J.G., Collins, L., Wemmer, C., Bush, M., and Wildt, D.E., 1991, Captive breeding of black-footed ferrets (*Mustela nigripes*) and comparative reproductive efficiency in 1-year old versus 2-year old animals: Journal of Zoo and Wildlife Medicine, v. 22, p. 96–106.

Curry, P.T., Ziemer, T., Van der Horst, G., Burgess, W., Straley, M., Atherton, R.W., and Kitchin, R.M., 1989, A comparison of sperm morphology and silver nitrate staining characteristics in the domestic ferret and the black-footed ferret: Gamete Research, v. 22, p. 27–36.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Hillman, C.N., and Carpenter, J.W., 1983, Breeding biology and behavior of captive black-footed ferrets, *Mustela nigripes*: International Zoo Yearbook, v. 23, p. 186–191.

Holt, W.V., Bennett, P.M., Volobouev, V., and Watson, P.F., 1996, Genetic resource banks in wildlife conservation: Journal of Zoology, v. 238, p. 531–544.

Howard, J.G., 1993, Semen collection and analysis in nondomestic carnivores, *in* Fowler, M.E., ed., Zoo and wild animal medicine—current therapy III: Philadelphia, W.B. Saunders Co., p. 390–399.

Howard, J.G., 1999, Assisted reproductive techniques in nondomestic carnivores, *in* Fowler, M.E., and Miller, R.E., eds., Zoo and wild animal medicine IV: Philadelphia, W.B. Saunders Co., p. 449–457.

Howard, J.G., Bush, M., Morton, C., Morton, F., and Wildt, D.E., 1991, Comparative semen cryopreservation in ferrets (*Mustela putorius furo*) and pregnancies after laparoscopic intrauterine insemination with frozen-thawed spermatozoa: Journal of Reproduction and Fertility, v. 92, p. 109–118.

Howard, J.G., Kwiatkowski, D.R., Williams, E.S., Atherton, R.W., Kitchin, R.M., Thorne, E.T., Bush, M., and Wildt, D.E., 1996, Pregnancies in black-footed ferrets and Siberian polecats after laparoscopic artificial insemination with fresh and frozen-thawed semen, *in* Proceedings of the American Society of Andrology, Journal of Andrology, supplement P-51, abstract 115.

Howard, J.G., Wolf, K.N., Marinari, P.E., Kreeger, J.S., Anderson, T.R., Vargas, A., and Wildt, D.E., 1998, Delayed onset of sperm production in 1-year old male black-footed ferrets, *in* Proceedings of the Society for the Study of Reproduction, Biology of Reproduction, supplement 58, abstract 170, p. 124.

Johnston, L.A., and Lacy, R.C., 1995, Genome resource banking for species conservation—selection of sperm donors: Cryobiology, v. 32, p. 68–77.

Kidder, J., Roberts, P.J., Simkin, M.E., Foote, R.H., and Richmond, M.E., 1999, Nonsurgical collection and nonsurgical transfer of preimplantation embryos in the domestic rabbit (*Oryctolagus cuniculus*) and domestic ferret (*Mustela putorius furo*): Journal of Reproduction and Fertility, v. 116, p. 235–242.

Mead, R.A., Joseph, M.M., and Neirinckx, S., 1988, Optimal dose of human chorionic gonadotropin for inducing ovulation in the ferret: Zoo Biology, v. 7, p. 263–267.

Mead, R.A., Neirinckx, S., and Czekala, N.M., 1990, Reproductive cycle of the steppe polecat (*Mustela eversmanni*): Journal of Reproduction and Fertility, v. 88, p. 353–360.

Miller, B., Biggins, D., Hanebury, L., and Vargas, A., 1993, Reintroduction of the black-footed ferret, *in* Mace, G., Olney, P., and Feisner, A., eds, Creative conservation—interactive management of wild and captive animals: London, Chapman and Hall, p. 455–464.

Miller, B., Reading, R.P., and Forrest, S., eds., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Miller, B.J., Anderson, S., DonCarlos, M.W., and Thorne, E.T., 1988, Biology of the endangered black-footed ferret (*Mustela nigripes*) and the role of captive propagation in its conservation—Canadian Journal of Zoology, v. 66, p. 765–773.

Miller, B.J., and Anderson, S.H., 1990, Comparison of black-footed ferret (*Mustela nigripes*) and domestic ferret (*M. putorius furo*) courtship activity: Zoo Biology, v. 9, p. 201–210.

Neal, J.B., Murphy, B.D., Moger, W.H., and Oliphant, L.W., 1977, Reproduction in the male ferret—gonadal activity during the annual cycle—recrudescence and maturation: Biology of Reproduction, v. 17, p. 380–385.

O'Brien, S.J., Martenson, J.S., Eichelberger, M.A., Thorne, E.T., and Wright, F., 1989, Genetic variation and molecular systematics of the black-footed ferret, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds, Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 21–33.

Reading, R.P., and Kellert, S.R., 1993, Attitudes toward a proposed reintroduction of black-footed ferrets (*Mustela nigripes*): Conservation Biology, v. 7, p. 569–580.

Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., 1989, Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, 302 p.

Thorne, E.T., and Oakleaf, B., 1991, Species rescue for captive breeding—black-footed ferret as an example, *in* Gipps, J.H.W., ed., Beyond captive breeding—re-introducing endangered mammals to the wild: Oxford, Clarendon Press, p. 241–261.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

Van der Horst, G., Curry, P.T., Kitchin, R.M., Burgess, W., Thorne, E.T., Kwiatkowski, D., Parker, M., and Atherton, R.W., 1991, Quantitative light and scanning electron microscopy of ferret sperm: Molecular Reproduction and Development, v. 30, p. 232–240.

Wildt, D.E., Brown, J.L., and Howard, J.G., 2001a, Role of reproductive sciences in carnivore conservation, *in* Gittleman, J.L., Funk, S.M., MacDonald, D.W., and Wayne, R.K., eds., Carnivore conservation: Cambridge, Cambridge University Press, p. 359–371.

Wildt, D.E., Bush, M., Morton, C., Morton, F., and Howard, J.G., 1989, Semen characteristics and testosterone profiles in ferrets kept in long-day photoperiod, and the influence of hCG timing and sperm dilution on pregnancy rate after laparoscopic insemination: Journal of Reproduction and Fertility, v. 86, p. 349–358.

Wildt, D.E., Ellis, S., and Howard, J.G., 2001b, Linkage of reproductive sciences—from 'quick fix' to 'integrated' conservation, *in* Concannon, P.W., England, G.C.W., Farstad, W., Linde-Forsberg, C., Verstegen, J.P., and Doberska, C., eds., Advances in reproduction in dogs, cats and exotic carnivores: Colchester, Journal of Reproduction and Fertility, Ltd., p. 295–307.

Wildt, D.E., and Goodrowe, K.L, 1989, The potential for embryo technology in the black-footed ferret, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 160–176.

Wildt, D.E., Rall, W.F., Critser, J.K., Monfort, S.L., and Seal, U.S., 1997, Genome resource banks—living collections for biodiversity conservation: BioScience, v. 47, p. 689–698.

Wildt, D.E., and Roth, T.L., 1997, Assisted reproduction in managing and conserving threatened felids: International Zoo Yearbook, v. 35, p. 164–172.

Wildt, D.E., Schiewe, M.C., Schmidt, P.M., Goodrowe, K.L., Howard, J.G., Phillips, L.G., O'Brien, S.J., and Bush, M., 1986, Developing animal model systems for embryo technologies in rare and endangered wildlife: Theriogenology, v. 25, p. 33–51.

Williams, E.S., Thorne, E.T., Appel, M.J.G., and Belitsky, D.W., 1988, Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming: Journal of Wildlife Diseases, v. 24, p. 385–398.

Williams, E.S., Thorne, E.T., Kwiatkowski, D.R., Anderson, S.T., and Lutz, K., 1991, Reproductive biology and management of captive black-footed ferrets (*Mustela nigripes*): Zoo Biology, v. 10, p. 383–398.

Williams, E.S., Thorne, E.T., Kwiatkowski, D.R., Lutz, K., and Anderson, S.T., 1992, Comparative vaginal cytology of the estrous cycle of black-footed ferrets (*Mustela nigripes*), Siberian polecats (*M. eversmanni*), and domestic ferrets (*M. putorius furo*): Journal of Veterinary Diagnostic Investigations, v. 4, p. 38–44.

Wolf, K.N., Wildt, D.E., Vargas, A., Marinari, P.E., Kreeger, J.S., Ottinger, M.A., and Howard, J.G., 2000a, Age-dependent changes in sperm production, semen quality and testicular volume in black-footed ferrets (*Mustela nigripes*): Biology of Reproduction, v. 63, p. 179–187.

Wolf, K.N., Wildt, D.E., Vargas, A., Marinari, P.E., Ottinger, M.A., and Howard, J.G., 2000b, Reproductive inefficiency in male black-footed ferrets (*Mustela nigripes*): Zoo Biology, v. 19, p. 528.

The Genetic Legacy of the Black-footed Ferret: Past, Present, and Future

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Abstract

The black-footed ferret (*Mustela nigripes*) evolved in Beringia sometime in the early to middle Pleistocene. By 35,000 years before present the species was distinct from its sister taxon, the Siberian polecat (*Mustela eversmannii*). Genetic analysis revealed that historical populations had restricted gene flow prior to human disturbance, which had consequences for the conservation of genetic diversity in the species. Most genetic diversity in the species was lost when Great Plains populations were extirpated, leaving the last surviving population genetically distinct and depauperate. Further genetic losses occurred when almost half of the animals captured from the last population failed to breed in captivity. Once established in captivity, however, maintenance of remaining genetic diversity was within the goals of genetic management mandated by the recovery plan. Reintroduced populations of black-footed ferrets maintained genetic diversity, but were slightly differentiated from one another because of differences in population founders. Wild-born animals were less inbred than captive-released animals, suggesting that inbreeding avoidance mechanisms may operate in the wild. Although much diversity has been lost, inbreeding depression has not been confirmed. Future management efforts should maintain vigilance to conserve remaining genetic diversity both in captivity and in reintroduced populations.

Keywords: captive breeding, genetic diversity, genetic drift, Pleistocene refugia, population bottleneck, reintroduction

Introduction

Eighteen years have passed since the first genetic study of the black-footed ferret (*Mustela nigripes*) was completed (Kilpatrick and others, 1986). Although techniques have advanced and our understanding of genetic processes has expanded, the story revealed by this species' genes remains unwaveringly clear: the genetic uniformity measured in this species is unprecedented and rivaled by perhaps only one other carnivore, the cheetah (*Acinonyx jubatus*; O'Brien and others, 1983). Unlike the cheetah, however, whose Holocene population bottleneck remains shrouded in mystery, the black-footed ferret's demise was witnessed and documented by museum collectors, commercial trappers, animal control agents, and biologists (Anderson and others, 1986), providing a clear understanding of the demography of the bottleneck. Although the dramatic nature of the bottleneck was unfortunate for conservation of the species, it provides conservation-based science with the opportunity to study the genetic consequences of rapid and dramatic population loss outside of the laboratory setting.

Population bottlenecks occur when population size is rapidly reduced; the severity of a bottleneck depends on the minimum population size attained and the duration of time it remained small (Frankham and others, 2002). Although the immediate consequence of small population size is increased risk of extinction as a result of demographic stochasticity, long-term consequences result from reduced genetic diversity and increased inbreeding (Frankel and Soulé, 1981). By increasing the expression of deleterious alleles, inbreeding reduces individual fitness, further increasing the likelihood of extinction. Inbreeding depression caused by a population bottleneck has been documented in a variety of species, including the Florida panther (*Puma concolor coryi*; Roelke and others, 1993), fritillary butterflies (*Melitaea cinxia*; Saccheri and others, 1998), and koalas (*Phascolarctos cinereus*; Seymour and others, 2001). Reduced genetic diversity also has the insidious and difficult to measure effect of reducing a species' ability to adapt to a changing environment. Examples in the literature are few but include endemic rainforest fruitflies (*Drosophila* spp.; Hoffman and others, 2003).

The black-footed ferret experienced serious population decline beginning in the mid- to late 1800s as people migrated west and converted grasslands to agriculture. By 1981 only one population remained, and the species reached its nadir in 1987 when the last of 18 individuals were taken into captivity from Meeteetse, Wyo. (Clark, 1994). This was the first time the U.S. Fish and Wildlife Service (FWS) had managed an endangered species by removing all living individuals from the wild. Ironically, FWS made that decision twice in 1987, when the last remaining California condors (*Gymnogyps californianus*; Seal, 1989; Snyder and Snyder, 2000) were also removed from the wild and placed in a captive breeding program. Unfortunately, animal husbandry practices were not fully

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established in the initial years of captive breeding, and only seven founding ferrets are represented in the current captive population (Garell and others, 1998). Nonetheless, more than 4,000 individuals have been produced, and today approximately 240 animals exist in captivity and 500 in the wild. With a founder genome equivalent (the number of unique genomes represented in the current population) of 4.1 (Russell and others, 1994), the species currently contains a fraction of the genetic diversity once present.

Several demographic events transpired to reduce the population size of this species. Habitat conversion, poisoning campaigns aimed at prairie dogs (*Cynomys* spp.), and exotic diseases decreased the population by 99 percent over approximately 100 years. In the last historical population, simultaneous epizootics of canine distemper virus and sylvatic plague (caused by the bacterium *Yersinia pestis*) caused dramatic population decline in less than a year. In order to understand the consequences of these demographic events, one must first understand the context in which they occurred. How much genetic diversity did the species have prior to anthropogenic disturbance? How much genetic diversity did black-footed ferrets have prior to the bottleneck of the Meeteetse population? How did population structure affect the rate of loss of genetic diversity? Once ferrets were taken into a captive breeding program, how well was the remaining genetic diversity conserved? Finally, as reintroduced populations continue to be established, it is crucial to understand how the process of reintroduction affects genetic diversity and structure. In the following chapter, I synthesize what is known about the genetic legacy of this species as it passed through the processes of population bottleneck, captive management, and reintroduction.

Pleistocene Colonization of North America

The black-footed ferret is a relatively recent immigrant to North America via the Bering land bridge (Youngman, 1994). The earliest fossil record of a black-footed ferret in North America is from Cathedral Cave in eastern central Nevada (Owen and others, 2000). This specimen dates approximately 800,000 years before present based on paleomagnetic data and biochronology of arvicoline rodents collected at the site (Owen and others, 2000). In support of a middle Pleistocene invasion, molecular clock estimates based on 41 isozymes suggest that the black-footed ferret split from its sister species the Siberian polecat (Mustela eversmannii) between 0.5 and 2 million years ago (O'Brien and others, 1989). Thus it appears that the ancestral black-footed ferret crossed the land bridge approximately 1 to 2 million years ago. The species gained access to the grasslands and shrublands of North America via an interglacial, ice-free corridor (Anderson, 1989; Youngman, 1994) and was established at least as far south as Nevada by 800,000 years ago. Once established, the species spread rapidly throughout the Great Plains. By 35,000 years before present the black-footed ferret was morphologically distinguishable from the Siberian polecat. In fact, the two species appear to have existed sympatrically; fossils of both species found in eastern Beringia as recently as 35,000 years ago suggest a period of secondary contact after differentiation (Youngman, 1994).

Molecular data suggest that black-footed ferret populations had restricted gene flow and high population differentiation that was influenced by both natural history and the ebb and flow of Pleistocene glaciers (Wisely and others, 2002). Genetic variation becomes partitioned among subpopulations when isolating mechanisms, such as Pleistocene glaciers and unsuitable habitat, prevent gene flow and increase genetic drift (Frankham and others, 2002). Using microsatellite markers, Wisely and others (2002) reported an average F_{ST} of 0.53. F_{ST} is a pairwise measure of genetic variation that is partitioned among populations. This parameter measures genetic structure and gene flow between subpopulations and ranges in value from 0 (no allelic differentiation or structure) to 1 (maximum allelic divergence). The value found for black-footed ferrets is one of the highest reported for a mammalian carnivore and likely reflects aspects of their unusual ecology. Their diminutive body size, coupled with their semifossorial lifestyle, likely limited their dispersal capabilities (when compared to other carnivorans) and therefore induced genetic drift within populations and created genetic differentiation among populations (Wisely and others, 2002). Subpopulation isolation was likely exasperated by habitat barriers that formed during glacial maxima.

Historical Genetic Diversity and Structure

The historical population structure of the black-footed ferret in North America greatly influenced the amount of genetic diversity that was lost. The magnitude of loss of genetic diversity was exasperated by the especially isolated nature of the last population. Located on the periphery of the historical distribution near the town of Meeteetse, Wyo. (Hillman and Clark, 1980), this population was likely a refugium during the last glacial maximum and remained isolated from other populations throughout the Holocene (Wisely and others, 2002). Measures of genetic distance used to estimate genetic differences among black-footed ferrets from three historical populations confirm that the Meeteetse population was the most highly differentiated and therefore isolated of the three populations (Wisely and others, 2002). Thus, when ferret populations from the Great Plains were extirpated, the majority of genetic diversity found in the species was lost (table 1, fig. 1). Indeed, the Meeteetse population was different enough from other ferret populations that the addition of even four individuals from Mellette County, S. Dak. (the second to last population of black-footed ferrets), would have increased allelic diversity in extant ferrets by 50 percent (Wisely and others, 2002).

Table 1. Observed (H_o) and expected (H_e) heterozygosities for 14 microsatellite loci in black-footed ferrets (*Mustela nigripes*) from Wyoming, South Dakota, and Kansas combined (representing the species prior to disturbance; *n* = 20) and from Wyoming only (*n* = 12), and HWE *P*, the probability associated with an exact test of Hardy-Weinberg equilibrium. Seven of 14 loci were monomorphic in the Wyoming population. HWE was tested only in polymorphic loci from Wyoming. (From Wisely and others, 2002. Reprinted with permission of Oxford University Press, Oxford, U.K.)

Microsatellite loci names	Wyoming, South Dakota, Kansas		Wyoming only		
	H_o	H_e	H_o	H_e	HWE *P*
Mvis002	0.65	0.48	0.50	0.39	0.53
Mvis9700	0.33	0.36	0.33	0.39	1
Mvis072	0.47	0.65	0.67	0.58	0.77
Mer095	0.20	0.27	0.17	0.16	1
Mer049	0.35	0.69	0.50	0.51	1
Mvi57	0.10	0.54	0.17	0.16	1
Mvis022	0.11	0.63	0.08	0.23	0.13
Gg4	0.05	0.14	-	-	-
Mvis075	0.17	0.53	-	-	-
Mvi87	0.00	0.43	-	-	-
G1A	0.10	0.19	-	-	-
Mvi232	0.20	0.19	-	-	-
Mer022	0.11	0.45	-	-	-
Mer009	0.06	0.06	-	-	-

Diversity and Structure in Captivity

Although Meeteetse animals were first captured in 1985, successful breeding was not achieved until 1987 (Clark, 1994). Of the 18 animals that survived in captivity, only 8–11 founders (unknown paternity of some wild-caught litters created some uncertainty as to the exact number) were initially represented in the pedigree; 20 years later, only 7 founders are represented in the extant population (Garell and others, 1998). The consequences of this bottleneck were measurable. Had 5 more of the original 18 ferrets bred successfully, genetic diversity of the extant population would have increased by 30 percent (fig. 1; Wisely and others, 2002). Once animal husbandry was understood and disease concerns were alleviated, the population quickly expanded, and the remaining genetic diversity was conserved (Wisely and others, 2003).

The dramatic loss of approximately 90 percent of the species' genetic diversity necessitated conservation of that which remained. Because all captive populations are susceptible to problems associated with small population size, including inbreeding, inbreeding depression, and genetic drift (de Boer, 1994), management of the remaining genetic variation was a high priority (Ballou and Oakleaf, 1989). Various approaches have been used to maximize retention of genetic variability; for the black-footed ferret, the mean kinship strategy augmented with line breeding of underrepresented founders was recommended (Ballou and Oakleaf, 1989). Briefly, mean kinship strategy finds suitable breeding pairs that maximize the representation of the most underrepresented founders of the captive population. Over time, this strategy is predicted to maximally conserve genetic diversity. Empirically, it appears that this strategy has succeeded in adequately preserving genetic diversity. Founders' genes were more evenly represented in the captive population in 1999 than in the first generation of captive black-footed ferrets (fig. 2; Wisely and others, 2003), and even representation of founders maximally conserves genetic diversity in a pedigreed population. Likewise, a pedigree-based estimate of loss of heterozygosity was 12 percent, which meets the goal established by the American Zoo and Aquarium Association's Species Survival Plan® of retaining 80 percent of the genetic diversity of the founding population for 25 years (Garell and others, 1998). Molecular-based estimates revealed no loss of allelic diversity; all alleles present in the founders were present in the extant population (Wisely and others, 2003).

Diversity and Structure of Reintroduced Populations

Once captive-born animals were released into the wild, further challenges faced the recovery program. A successful captive breeding reintroduction program involves substantive

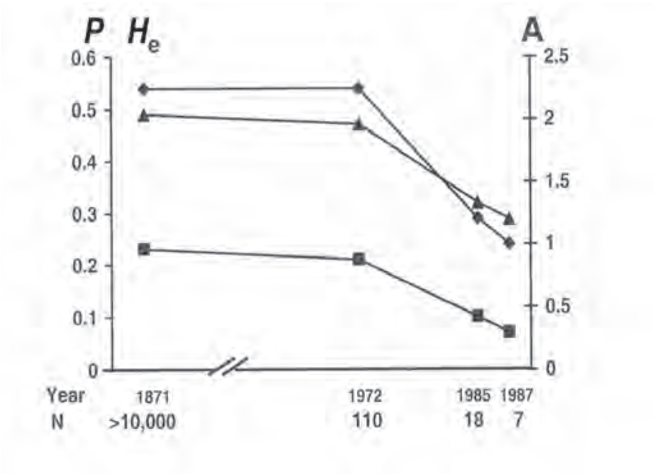

Figure 1. A timeline of genetic diversity in the black-footed ferret (*Mustela nigripes*). A, the average number of alleles per locus (triangle); H_e, expected heterozygosity (diamond); and P, the proportion of polymorphic loci (square) were at their highest values in 1871. In 1972 only two populations remained, in Mellette County, S. Dak., and Meeteetse, Wyo. Note that although many populations throughout the Great Plains were extirpated, genetic diversity did not appreciably decrease. With the loss of the Mellette County population, substantial amounts of genetic diversity were lost. Only the Meeteetse population remained in 1982. Further loss of genetic diversity occurred because of a bottleneck in the last population from 1982 to 1987. (From Wisely and others, 2002. Reprinted with permission of Oxford University Press, Oxford, U.K.)

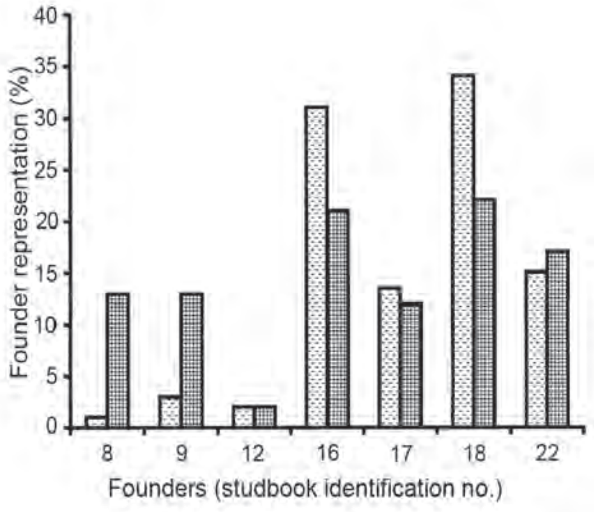

Figure 2. Founder representation in the first generation of captive breeding (i.e., all the direct descendants) (dotted bars) and in 1999, after 14 years of captive breeding (cross-hatched bars) of black-footed ferrets (*Mustela nigripes*). Only founders with genes represented in the extant population are considered. (From Wisely and others, 2003. Reprinted with permission of Wiley-Liss, Hoboken, N.J.)

but reconcilable tradeoffs. Demographic and genetic attributes affect the success of reintroduced populations (Jiménez and others, 1994; FitzSimmons and others, 1997), yet selection of animals for release removes them and their potentially unique genes from the captive breeding pool. This sets up a potential conflict between the goals of captive breeding and reintroduction (Earnhardt, 1999). Because of the tenuous nature of the early captive breeding program and the recognition that captive breeding would need to be maintained for many years, inbred animals and animals with a mean kinship >0.125 were designated for release (Ballou and Oakleaf, 1989). This strategy would maximize retention of genetic diversity in the captive population.

Inbreeding in 1991, estimated from pedigree analysis, was higher in released captive-bred animals ($F = 0.092$) than in animals retained in the captive population ($F = 0.052$; Russell and others, 1994), as would be expected by the designation criteria for animals retained versus released from the captive population. By 1999, overall inbreeding was higher (as would be expected in a small, closed population), but the difference between captive breeders and captive releases was negligible ($F = 0.12$ and 0.11, respectively; Wisely and others, 2003). The gap between breeders and releases was closed because founder genes were more evenly represented in the 1999 than in the 1991 captive population (fig. 2), resulting in a panmictic population. Equal founder representation reduced the variance in mean kinship of individuals, which in turn decreased the difference in genetic composition between breeders and releases (Wisely and others, 2003).

As of 1999, no difference in genetic diversity had been detected between captive-reared releases and their wild descendants from Charles M. Russell National Wildlife Refuge, Mont., and Conata Basin, S. Dak. (table 2; Wisely and others, 2003). This finding suggests that initial releases and subsequent augmentation were sufficient to halt drift-induced losses in diversity. Small but statistically significant population differentiation ($F_{ST} = 0.09$, 95 percent CI = 0.04–0.13) between wild descendants of two reintroduced populations suggested that even with augmentation of captive animals to the reintroduced population, these two populations had measurable genetic differences attributable to random differences in the founders of each reintroduction site (Wisely and others, 2003). Whether this statistically significant difference is also biologically significant is difficult to say (Hedrick, 1999). It is likely, however, that, as populations grow and augmentation ceases, continuing genetic drift will decrease genetic diversity within populations and increase genetic distance among populations.

Because wild-born animals were descended from animals with higher than average mean kinship and inbreeding (as calculated from the pedigree and estimated from microsatellites), it was predicted that the offspring would be inbred. In fact, this was not the case (table 2; Wisely and others, 2003). This result was surprising inasmuch as free ranging populations were smaller than the captive population, released animals were the descendants of overrepresented individuals,

Table 2. Measures of genetic diversity, H_o, the observed heterozygosity, and H_e, the expected heterozygosity, for five groups of black-footed ferrets (*Mustela nigripes*), and HWE *P*, the probability of heterozygote deficiencies (an indicator of inbreeding) within groups. H_e and H_o values were averaged over the seven microsatellite loci that were polymorphic in the historical Wyoming population. Each of the seven loci had two alleles per locus in each group of ferrets. Both captive breeders and captive releases showed evidence of inbreeding as predicted by pedigree-based methods. (From Wisely and others, 2003. Reprinted with permission of Wiley-Liss, Hoboken, N.J.)

Group	*n*	H_o	H_e ± 2 SE	HWE *P*
Founders	7	0.40	0.33 ± 0.14	0.76
Captive breeders	29	0.32	0.41 ± 0.12	0.03
Captive releases	36	0.31	0.38 ± 0.14	0.01
Wild, Montana	81	0.33	0.33 ± 0.14	0.47
Wild, South Dakota	41	0.43	0.38 ± 0.12	0.87

and litter mates often were released together. A possible explanation for the lack of inbreeding in the wild populations is a behavioral response of inbreeding avoidance. Several researchers have proposed that closely related individuals avoid mating in such taxa as black-tailed prairie dogs (*Cynomys ludovicianus*; Hoogland, 1982), olive baboons (*Papio anubis*; Packer, 1979), and the marsupial genus *Antechinus* (Cockburn and others, 1985). Given that the reintroduced founding populations were small and that black-footed ferrets avoided close kin matings, survival and reproduction of founding populations may have been less than optimal as reintroduced individuals avoided breeding with one another and dispersed to find unrelated mates (Wisely and others, 2003).

The Future

The consequence of dramatic loss of genetic diversity in a species is unclear. Some taxa, such as felids, are highly susceptible to inbreeding depression, while other taxa appear unaffected (Ralls and Ballou, 1983; Lacy, 1997). Small, inbreeding populations have a higher rate of expression of deleterious alleles, which can lead to extinction when the forces of genetic drift are greater than natural selection. When selection exceeds drift, however, small, inbreeding populations can purge deleterious alleles, ultimately making them less susceptible to inbreeding depression. To date, no physiological abnormalities have been linked to inbreeding depression in black-footed ferrets, although abnormalities exist (Howard and others, this volume). Indeed, fecundity of females (measured as kits surviving per litter) was virtually the same (3.1–3.3 kits per female) for animals observed in the historical populations of Mellette County, S. Dak. (Hillman and Carpenter, 1980), and Meeteetse, Wyo. (Forrest and others, 1988), and the reintroduced population in Conata Basin, S. Dak. (U.S. Department of Agriculture, 2000).

Without question the two biggest hurdles to recovery of this species are lack of suitable habitat for reintroduction and sylvatic plague (Conservation Breeding Specialist Group, 2004). Where ample, plague-free habitat exists, populations appear to flourish despite reduced genetic diversity. The dramatic loss of genetic diversity in this species should not discourage biologists from planning for recovery. With careful management of remaining genetic resources, this species will likely persist. Continued, vigilant conservation of genetic diversity in the captive population will be critical to the long-term success of this recovery effort. Likewise, genetic management of the reintroduced populations will be critical once populations become self-sustaining. Currently, only two populations are self-sustaining: those of Shirley Basin, Wyo., and Conata Basin, S. Dak. All other reintroduction sites rely on yearly augmentation to maintain their populations. Translocations for genetic augmentation may be necessary if reintroduced populations lose genetic diversity because of drift.

The dramatic loss of genetic diversity in this endangered species should serve as a reminder to conservation practitioners that proactive management of population structure (conserving as many individuals from as many geographic locations as possible) can have a profound effect on the conservation of genetic resources for a species. Furthermore, rapid breeding of as many founders as possible within the first few generations of captive breeding will maximize the retention of the remaining genetic diversity and increase the likelihood of persistence into the future.

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References Cited

Anderson, E., 1989, The phylogeny of mustelids and the systematics of ferrets, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 10–20.

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Ballou, J.D., and Oakleaf, R., 1989, Demographic and genetic captive-breeding recommendations for black-footed ferrets, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 247–267.

Clark, T.W., 1994, Restoration of the endangered black-footed ferret—a 20-year overview, *in* Bowles, M.L., and Whelan, C.J., eds., Restoration of endangered species—conceptual issues, planning, and implementation: New York, Cambridge University Press, p. 272–297.

Cockburn, A., Scott, M.P., and Scott, D.J., 1985, Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae): Animal Behaviour, v. 33, p. 908–915.

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

de Boer, L.E.M., 1994, Development of coordinated genetic and demographic breeding programmes, *in* Olney, P.J.S., Mace, G.M., and Feistner, A.T.C., eds., Creative conservation: interactive management of wild and captive animals: New York, Chapman and Hall, p. 304–311.

Earnhardt, J.M., 1999, Reintroduction programmes—genetic trade-offs for populations: Animal Conservation, v. 2, p. 279–286.

FitzSimmons, N.N., Buskirk, S.W., and Smith, M.H., 1997, Genetic changes in reintroduced Rocky Mountain bighorn sheep populations: Journal of Wildlife Management, v. 61, p. 863–872.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–173.

Frankel, O.H., and Soulé, M.E., 1981, Conservation and evolution: New York, Cambridge University Press, 327 p.

Frankham, R., Ballou, J.D., and Briscoe, D.A., 2002, Introduction to conservation genetics: New York, Cambridge University Press, 617 p.

Garell, D., Vargas, A., and Marinari, P., 1998, Black-footed ferret species survival plan—annual report 1997: Bethesda, Md., American Zoo and Aquarium Association, 3 p.

Hedrick, P.W., 1999, Perspective—highly variable loci and their interpretation in evolution and conservation: Evolution, v. 53, p. 313–318.

Hillman, C.N., and Carpenter, J.W., 1980, Masked mustelid: Nature Conservancy News, March–April, p. 20–23.

Hillman, C.N., and Clark, T.W., 1980, Black-footed ferret (*Mustela nigripes*): Mammalian Species, v. 126, p. 1–3.

Hoffman, A.A., Hallas, R.J., Dean, J.A., and Schiffer, M., 2003, Low potential for climatic stress adaptation in a rainforest *Drosophila* species: Science, v. 301, p. 100–102.

Hoogland, J.L., 1982, Prairie dogs avoid extreme inbreeding: Science, v. 215, p. 1639–1641.

Jiménez, J.A., Hughes, K.A., Alaks, G., Graham, L., and Lacy, R.C., 1994, An experimental study of inbreeding depression in a natural habitat: Science, v. 266, p. 271–273.

Kilpatrick, C.W., Forrest, S.C., and Clark, T.W., 1986, Estimating genetic variation in the black-footed ferret—a first attempt: Great Basin Naturalist Memoirs No. 8, p. 145–149.

Lacy, R.C., 1997, Importance of genetic variation to the viability of mammalian populations: Journal of Mammalogy, v. 78, p. 320–335.

O'Brien, S.J., Martenson, J.S., Eichelberger, M.A., Thorne, E.T., and Wright, F., 1989, Genetic variation and molecular systematics of the black-footed ferret, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 21–33.

O'Brien, S.J., Wildt, D.E., Goldman, D., Merril, C.R., and Bush, M., 1983, The cheetah is depauperate in biochemical genetic variation: Science, v. 227, p. 459–462.

Owen, P.R., Bell, C.J., and Mead, E.M., 2000, Fossils, diet, and conservation of black-footed ferrets (*Mustela nigripes*): Journal of Mammalogy, v. 81, p. 422–433.

Packer, C., 1979, Inter-troop transfer and inbreeding avoidance in *Papio anubis*: Animal Behaviour, v. 27, p. 1-36.

Ralls, K., and Ballou, J., 1983, Extinction—lessons from zoos, *in* Schonewald-Cox, C.M., Chambers, S.M., MacBryde, B., and Thomas, L., eds., Genetics and conservation—a reference for managing wild animal and plant populations: Menlo Park, Calif., Benjamin/Cummings, p. 164–184.

Roelke, M.E., Martenson, J.S., and O'Brien, S.J., 1993, The consequences of demographic reduction and genetic depletion in the endangered Florida panther: Current Biology, v. 3, p. 340–350.

Russell, W.C., Thorne, E.T., Oakleaf, R., and Ballou, J.D., 1994, The genetic basis of black-footed ferret reintroduction: Conservation Biology, v. 8, p. 263–266.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W., and Hanski, I., 1998, Inbreeding and extinction in a butterfly metapopulation: Nature, v. 392, p. 491–494.

Seal, U.S., 1989, Introduction, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. xi–xvii.

Seymour, A.M., Montgomery, M.E., Costello, B.H., Ihle, S., Johnsson, G., St. John, B., Taggart, D., and Houlden, B.A., 2001, High effective inbreeding coefficients correlate with morphological abnormalities in populations of South Australian koalas (*Phascolarctos cinereus*): Animal Conservation, v. 4, p. 211–219.

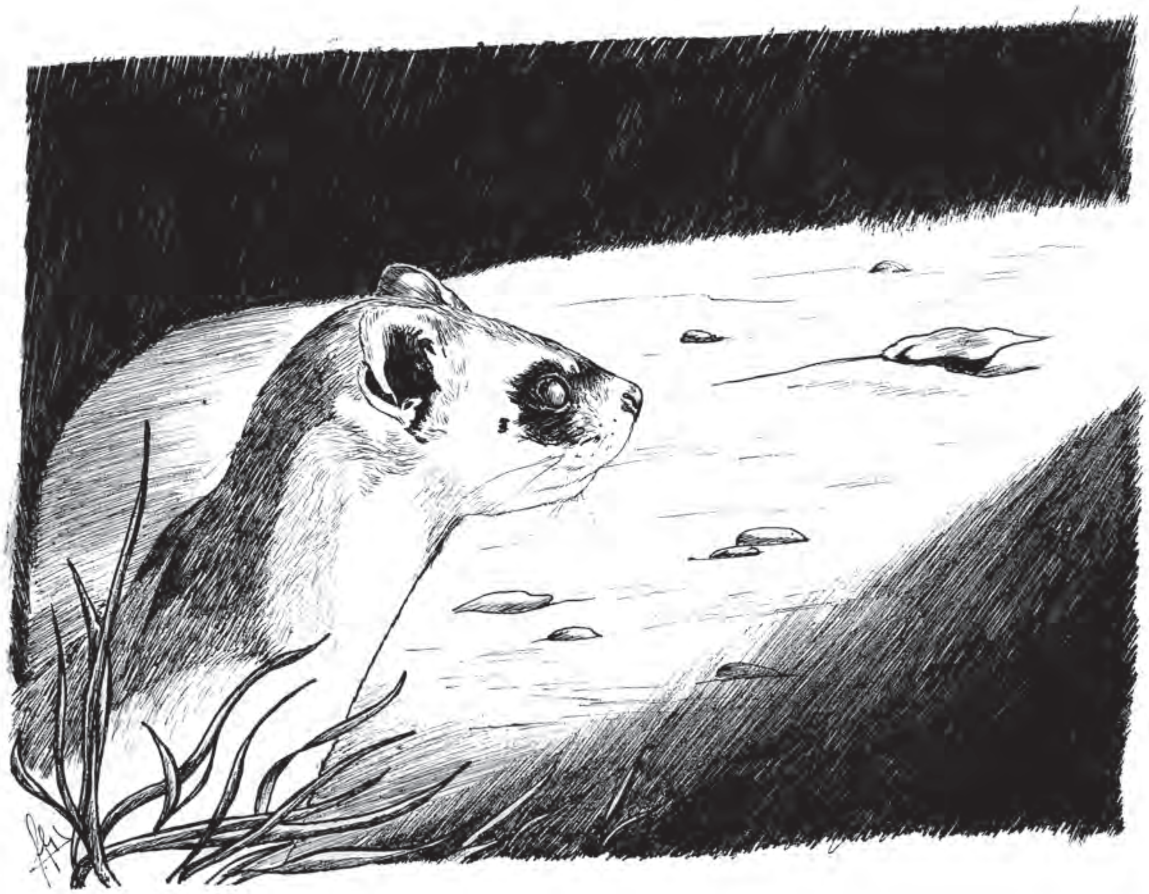
Snyder, N., and Snyder, H., 2000, The California condor—a saga of natural history and conservation: New York, Academic Press, 410 p.

U.S. Department of Agriculture, 2000, Summary of the black-footed ferret program—Conata Basin, Buffalo Gap National Grasslands, South Dakota: Wall, S. Dak., U.S. Department of Agriculture, Forest Service, 4 p.

Wisely, S.M., Fleming, M.A., McDonald, D.B., Buskirk, S.W., and Ostrander, E.A., 2002, Genetic diversity and fitness in black-footed ferrets before and during a bottleneck: Journal of Heredity, v. 93, p. 231–237.

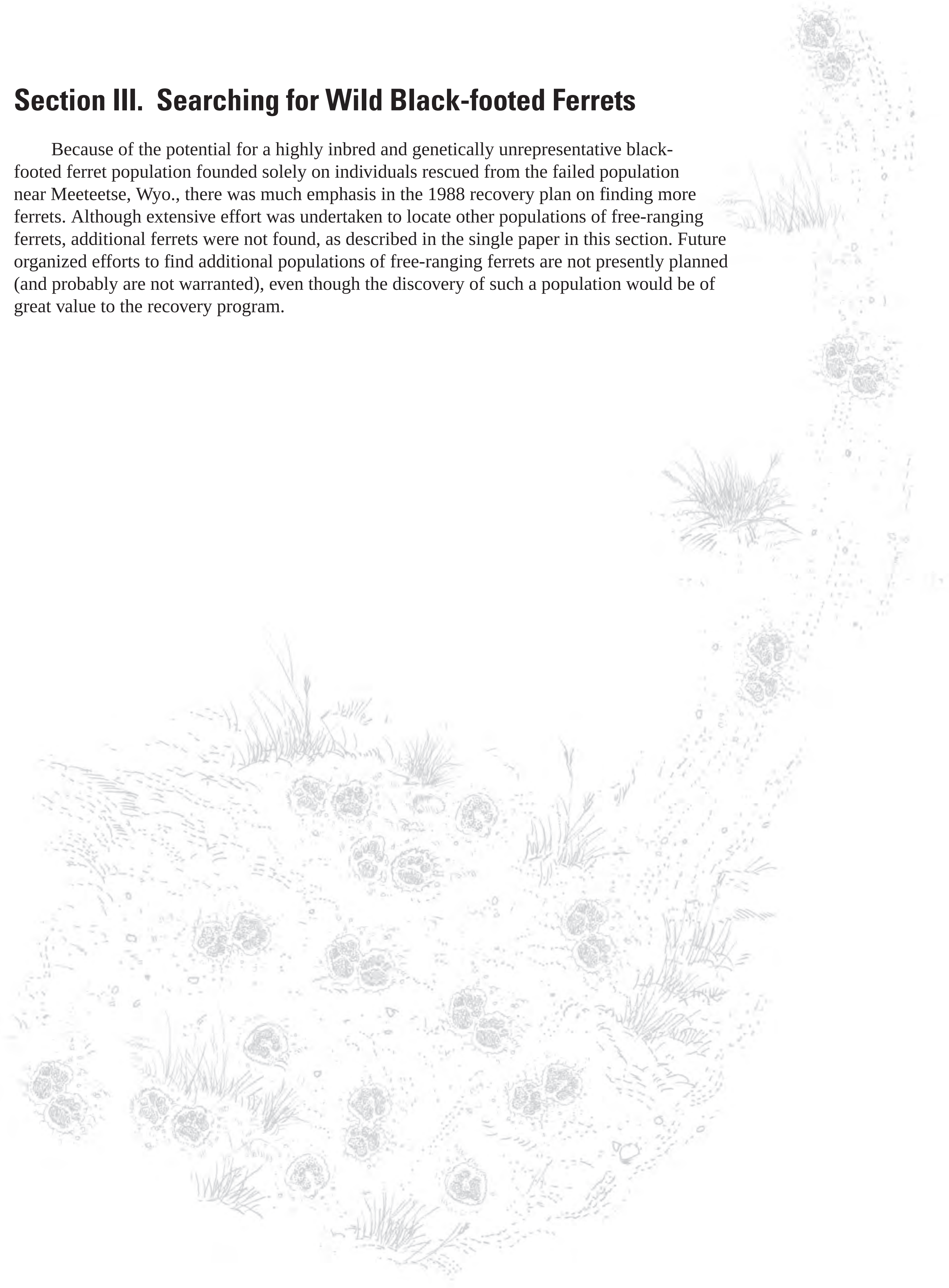
Wisely, S.M., McDonald, D.B., and Buskirk, S.W., 2003, Evaluation of the species survival plan and captive breeding program for the black-footed ferret: Zoo Biology, v. 22, p. 287–298.

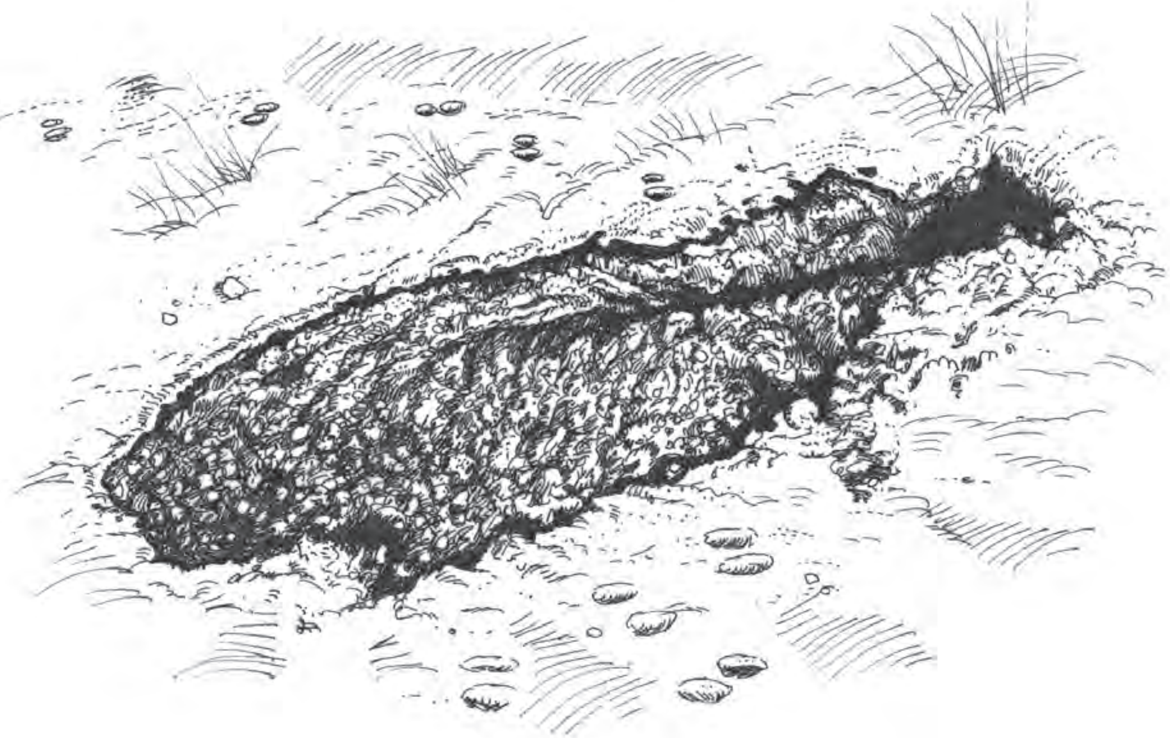
Youngman, P.M., 1994, Beringian ferrets—mummies, biogeography, and systematics: Journal of Mammalogy, v. 75, p. 454–461.



Section III. Searching for Wild Black-footed Ferrets

Because of the potential for a highly inbred and genetically unrepresentative black-footed ferret population founded solely on individuals rescued from the failed population near Meeteetse, Wyo., there was much emphasis in the 1988 recovery plan on finding more ferrets. Although extensive effort was undertaken to locate other populations of free-ranging ferrets, additional ferrets were not found, as described in the single paper in this section. Future organized efforts to find additional populations of free-ranging ferrets are not presently planned (and probably are not warranted), even though the discovery of such a population would be of great value to the recovery program.





A History of Searches for Black-footed Ferrets

By Louis R. Hanebury[1] and Dean E. Biggins[2]

Abstract

Studies of wild populations of black-footed ferrets (*Mustela nigripes*) in South Dakota in the 1960s, in Wyoming in the 1980s, and of captive-bred ferrets reintroduced to unoccupied habitat in Wyoming, South Dakota, and Montana in the 1990s contributed to our understanding of ferret behavior and improved techniques to find ferret populations. We chronicle the efforts of private, State, and Federal institutions that used these techniques to locate remaining populations of ferrets. During the 1980s, a renewed survey effort and solicitation of new sightings, coupled with a monetary reward program, failed to locate ferrets. We believe that the probability of finding ferrets from noncaptive stock is already small and diminishes with each passing year.

Keywords: black-footed ferret, *Mustela nigripes*, reward, sighting, spotlighting, survey technique

Introduction

The original recovery plan for the endangered black-footed ferret (*Mustela nigripes*) was approved in June 1978, and a revised recovery plan was approved in August 1988 (U.S. Fish and Wildlife Service, 1978, 1988). These plans established objectives and outlined steps for recovery that would provide for viable black-footed ferret populations in captivity and in the wild throughout the historical range. A common element in both plans was locating additional wild populations both for preservation and as a source of genetic diversity for the captive population. Brussard and Gilpin (1989) believed that any ferret still extant in the wild should be captured to augment the gene pool available to the captive breeding program. In addition, a multitude of individuals and organizations began work on delineating the historical range of the black-footed ferret, defining and identifying suitable habitat, and developing methodologies and techniques to find remaining populations. This paper presents an overview and update on efforts to locate an undiscovered population of ferrets.

Techniques for Finding a Wild Population of Ferrets

Methodologies to locate black-footed ferrets were first developed during the 11 years (1964–74) that a South Dakota population was studied (Hillman, 1968a,b; Sheets, 1970; Fortenbery, 1972; Hillman and Linder, 1973). Henderson and others (1969) presented important life history and behavioral characteristics, in addition to techniques for studying and locating black-footed ferrets. Nevertheless, Hillman and Linder (1973) emphasized the need to develop more efficient and conclusive techniques for detecting the presence of ferrets on prairie dog (*Cynomys* spp.) towns.

After the South Dakota population disappeared (the last wild ferrets in South Dakota were trapped in 1973; Carpenter and Hillman, 1978), the U.S. Fish and Wildlife Service's (FWS) Denver Wildlife Research Center (DWRC), Section of Wildlife Ecology on Public Lands, conducted black-footed ferret surveys on Federal lands (Martin and Schroeder, 1979, 1980; Smith and others, 1982; Martin, 1983). The objectives of those activities were to search for black-footed ferrets and test new or alternative methods for their detection. These methods included searches for sign (i.e., diggings, tracks, bones, scat, plugged burrows) by foot, horseback, snowmobile, and aircraft during daylight hours, as well as searches for ferrets at night using spotlights (on foot and from vehicles). Other techniques involved observing prairie dog behavior, using night vision equipment, and using scent dogs. A partial listing of such searches conducted by DWRC in Wyoming revealed a total of 1,166 person-hours of night searches with spotlights and much more time spent in day searches. Spotlight searches resulted in sightings of 54 coyotes (*Canis latrans*), 168 badgers (*Taxidea taxus*), and 15 long-tailed weasels (*Mustela frenata*), but there were no sightings of ferrets.

In 1981, a new population of black-footed ferrets was discovered near Meeteetse, Wyo. (Schroeder and Martin,

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1982). Four years of studies by FWS, Biota Research and Consulting, Inc., and the Wyoming Game and Fish Department increased our knowledge about locating and monitoring black-footed ferrets (Biggins, 1983; Biggins and Fagerstone, 1983; Clark and others, 1984b, 1986, 1988; Anderson and Inkley, 1985; Campbell and others, 1985; Clark, 1985; Richardson and others, 1985, 1987; Biggins and others, 1986; Fagerstone and Biggins, 1986; Johnson and others, 1986; Morkill, 1987). Although Clark and Campbell (1981a) had already devised ferret search guidelines, information from the Meeteetse studies assisted in formulating updated search techniques (Clark and others, 1984a, 1988). It also enabled FWS to develop black-footed ferret survey guidelines for compliance with the Endangered Species Act (ESA) of 1973, as amended (16 U.S.C. 1531–1543) (Schroeder, 1985; U.S. Fish and Wildlife Service, 1986). The Wyoming Cooperative Fish and Wildlife Research Unit, in cooperation with FWS, initiated workshops on black-footed ferret survey techniques in 1987. These workshops demonstrated the most current methodology for finding ferret populations. Training and certification were necessary to promote uniformity in techniques used by consultants and agency personnel. Workshops were held periodically until 1994, when Badlands National Park in South Dakota hosted the final training course. Today, skills to survey for black-footed ferrets are developed by individuals participating in field work at one of the active reintroduction sites in six States and in Mexico.

Guidelines were prepared by FWS to locate at least one animal of a population within three consecutive nights of spotlight surveys in a portion of the habitat. Using these survey guidelines (U.S. Fish and Wildlife Service, 1986), the probability of detecting ferrets was found to be high under simulated field conditions (Lindzey and Marinari, 1992; Marinari, 1992). Unpublished data from spotlight surveys for the reintroduced population of black-footed ferrets studied in the mid-1990s on the UL Bend National Wildlife Refuge in Montana confirmed the effectiveness of spotlight surveys using the FWS protocol (R. Matchett, oral commun., 2003). Spotlight surveys conducted while telemetry crews were monitoring radio-tagged ferrets suggested that over 90 percent of the ferrets above ground (as indicated by telemetry) were observed by search crews. Similarly, analysis of ferret observations over a 10-year period in the same area suggested high detectability of ferrets, given adequate search effort (Biggins, Godbey, Matchett, and others, this volume).

Henderson and others (1969) first proposed the use of a helicopter or airplane to locate ferrets during winter. Martin and Schroeder (1980) tested both fixed-wing aircraft and a helicopter for winter surveys to locate ferret sign. They found helicopters more practical because badger diggings were more easily found from helicopters. Biggins and Engeman (1986) found fixed-wing aircraft acceptable for locating ferret sign in winter. Aerial ferret surveys from helicopters were used effectively to survey the large white-tailed prairie dog (*C. leucurus*) complex in northwest Colorado and northeast Utah (U.S. Fish and Wildlife Service, 1989). Aerial surveys with helicopters or fixed-wing aircraft are currently used at some reintroduction sites and have been used successfully to locate ferrets that have dispersed into outlying prairie dog colonies (R. Matchett, oral commun., 2003).

In 1978, the DWRC began testing the use of scent dogs to locate black-footed ferrets or their sign (Conway and Dean, 1979; Southwest Research Institute, 1979; Martin and Schroeder, 1980). Two dogs were trained with scat obtained from captive black-footed ferrets held at FWS's (now U.S. Geological Survey's) Patuxent Wildlife Research Center in Laurel, Md. These dogs were later tested at Meeteetse, Wyo., in 1981 and demonstrated the ability to identify burrows known to be occupied by ferrets. Matchett and Smith (2001) successfully located reintroduced ferrets in Montana with trained scent dogs. Reindl (2004) proposed further testing and use of scent dogs in locating black-footed ferrets dispersing from reintroduction sites. Although variability of individual scent dog performance remains a problem, these studies indicate that dogs may be a useful supplement to spotlight surveys, particularly at sites where conventional search efficiency is poor. For example, scent dogs will be used during 2005 in remote, hard-to-search areas of the Colorado/Utah black-footed ferret reintroduction site (S. Reindl, oral commun., 2004).

Before the discovery of the Meeteetse population, Clark and Campbell (1983) tested a track station survey method using a variety of lures to detect nocturnal mammalian carnivores. Hammer and Anderson (1985) further studied the usefulness of track stations and numerous attractants to determine whether black-footed ferrets were present. Tracking and camera stations did not record any visitation in areas occupied by ferrets in the Meeteetse habitat. Scent stations were tested in ferret-occupied habitat in South Dakota with similar results (T. Livieri, oral commun., 2005). Scent attractants, track stations, and remote cameras have not been proven effective for locating ferrets in the wild.

Weasel-like scats have been collected during nocturnal and daylight surveys for ferrets and ferret sign (Henderson and others, 1969; Fortenbery, 1972; Martin and Schroeder, 1979; Clark and others, 1984a, 1988; Richardson and others, 1987). Typical black-footed ferret scat has been described, but identification of mustelid scat to species is often problematic. Johnson and others (1986) compared the fecal bile acid characteristics of known black-footed ferret scat and other known small carnivores and concluded that these acids did not enable positive identification of individual ferret scats. They did, however, suggest that ferret scats might be identifiable with reasonable confidence using gas-liquid chromatography, a technique yet to be thoroughly tested. Recent advances in DNA testing may provide a reliable and practical method to identify black-footed ferret scats where other sign is not discernible.

Reintroduced black-footed ferrets afforded renewed opportunities to gain knowledge on ferret behaviors, thereby increasing our ability to detect free-ranging ferrets. The first reintroduction of captive-raised black-footed ferrets at Shirley Basin, Wyo., yielded much information regarding behavior, dispersal, and postrelease survival (U.S. Fish and Wildlife Service, 1992; Wyoming Game and Fish Department, 1992, 1993, 1994, 1995; Oldemeyer and others, 1993). Subsequent reintroductions in South Dakota, Montana, Arizona, Colorado, and Utah have each added new data, which collectively have contributed to validating and refining effective search techniques.

Historical Sighting Reports and Surveys

Anderson and others (1986) provided an exhaustive summary of black-footed ferret specimens from North America, beginning with the first specimen collected by Audubon and Bachman in 1851. One of the earliest efforts to solicit black-footed ferret sightings occurred in 1952 (Cahalane, 1954). During the period 1946–53, 42 black-footed ferrets were reported from 42 localities, mostly in South Dakota, Montana, Nebraska, and Colorado (Cahalane, 1954). About one-third of the animals observed were found dead or were trapped (killed), shot, hit by vehicles, or died in captivity.

Cahalane's (1954) call for a life history study of the black-footed ferret was answered in 1964 with the discovery of the population in Mellette County, S. Dak. Before the South Dakota population disappeared, a black-footed ferret and prairie dog workshop in 1973 brought together State, Federal, and academic interests to present historical and current knowledge on prairie dogs and black-footed ferrets (Linder and Hillman, 1973). Eleven States, Federal agencies, and academic institutions provided information on available habitat, historical and recent black-footed ferret sightings, and efforts to locate additional populations (Clark, 1973; Grondahl, 1973; Henderson and Little, 1973; Lewis, 1973; Lewis and Hassien, 1973; Locke, 1973).

Kansas was one of the first States to have an active “Wanted: Black-footed Ferret” program. Historical ferret sightings, ferret specimen records, and new sighting reports formed the foundation for actively looking for additional populations (Henderson and Little, 1973). Letters and pamphlets were widely disseminated, supported by articles in local newspapers and magazines and by public radio and television announcements (Henderson, 1969). A color “Wanted Alive” poster was later produced and sent to all States within the original range of the black-footed ferret (appendix, fig. A1). Clark (1973, 1978, 1980) and Clark and Campbell (1981b) took a similar approach in Wyoming, identifying habitat and gathering historical and new specimen records and sighting reports. Campbell (1989) described searches to locate black-footed ferret populations conducted in Montana between 1984 and 1989. Crete (1985) discussed FWS's efforts to work with State agencies and private entities to find other wild populations of ferrets. A second major black-footed ferret workshop was held in 1984 in Laramie, Wyo. Federal and State agencies summarized new efforts to handle black-footed ferret sighting reports (Cada, 1985; Grode, 1985; Hammer, 1985; Hasenyager, 1985; Lengkeek, 1985).

Because of funding constraints and the lack of any legal mandate, searches for remaining populations of black-footed ferrets were at times limited. For example, despite the black-footed ferret's inclusion in the first list of rare and endangered wildlife by the U.S. Department of the Interior in 1964 (Clark, 1989), in the 1966 Endangered Species Preservation Act, and in the Endangered Species Conservation Act of 1969, there were no prohibitions of harm to a listed species (“taking” was prohibited only within national wildlife refuges) and therefore no requirements to determine whether black-footed ferrets were present prior to authorizing projects that might harm ferrets or modify their habitat. By 1965, the Department of the Interior had established a policy on precontrol surveys for prairie dog control programs throughout the range of the black-footed ferret on all classes of land (Berryman and Johnson, 1973). This policy was initially for, and first applied to, prairie dog control programs on Pine Ridge Indian Reservation in South Dakota (Hanson, 1988, 1993). New Mexico also initiated precontrol surveys for black-footed ferrets during that time (Hubbard and Schmitt, 1983). The policy on precontrol surveys was further refined by Executive Order 11643 (Berryman and Johnson, 1973). Jobman and Anderson (1985) reviewed other Federal authorities that might affect or be used in locating funds or facilitating ferret recovery activities. Schroeder (1988), however, noted the requirement for ferret surveys that was triggered by the ESA of 1973. Under section 7(a)(2), Federal agencies are required to consult with FWS to ensure that any action they authorize, fund, or carry out is not likely to jeopardize the continued existence of any endangered or threatened species or result in the destruction or adverse modification of a species' designated critical habitat. If suitable habitat (i.e., capable of supporting at least one black-footed ferret) is present within the action area, FWS has the authority to recommend that a ferret survey precede the project. In 1986, to provide some consistency in survey recommendations, FWS developed standard survey guidelines (Schroeder, 1985; U.S. Fish and Wildlife Service, 1986). When properly implemented, the prescribed strategy has good potential to detect a population of black-footed ferrets. Validating whether suitable habitat is occupied by ferrets is necessary to determine if an action may adversely affect the species. Because of the policy to include precontrol surveys for black-footed ferrets after 1965, the mandatory consultation requirements for Federal agencies in the ESA of 1973, and pesticide registration label statements (U.S. Environmental Protection Agency, 1987), surveys for black-footed ferrets by Federal agencies and their consultants have been occurring for 40 years. Black-footed ferret populations could have escaped detection because some surveys were inadequate or because some suitable habitats were never surveyed. Nonetheless, these surveys have covered large areas without finding a population of living ferrets (but they have resulted in discovery of old black-footed ferret remains).

In the initial black-footed ferret recovery plan (U.S. Fish and Wildlife Service, 1978), one recovery task was to map the amount of prairie dog habitat occupied by black-footed ferrets, to be accomplished by compiling sighting reports for each State within the historical range (Jobman and Anderson, 1981a). The FWS's Pierre, S. Dak., office was designated as the receiving station for all black-footed ferret sightings; this responsibility was moved to Grand Island, Nebr., in 1985. A questionnaire and letter requesting ferret sightings between January 1, 1970, and January 1, 1981, were sent to Provincial (Canadian), Federal, State, and private (tribal, industry, conservation, and recreation groups) institutions (Jobman and Anderson, 1981b), resulting in reports of 228 sightings. Sightings were classified as confirmed, probable, or unconfirmed. Periodic updates (W. Jobman, written commun., 1987–92) to the original report added the following additional sightings: 232 (1987), 51 (1988), 25 (1989), 26 (1990), 31 (1991), and 25 (1992). Partly because of the paucity of additional sightings, updates were discontinued in 1992, and sighting records are no longer formally maintained by FWS. Individual State or FWS offices may maintain records, however.

There are six reintroduced populations of black-footed ferrets that are designated nonessential, experimental in accordance with section 10(j) of the ESA. The black-footed ferret reintroduction sites represented the best habitat available and would seem to have been likely places to find any extant ferret populations. To comply with Section 10(j), all of these release sites were surveyed for resident black-footed ferrets. For example, there were 350 black-footed ferret surveys conducted on lands occupied by prairie dogs at the first site designated (Shirley Basin/Medicine Bow, Wyo.) to receive black-footed ferrets in 1991 (U.S. Fish and Wildlife Service, 1991). Other areas designated as nonessential, experimental populations received similar search efforts (U.S. Fish and Wildlife Service, 1993, 1994, 1996, 1998). Resident populations of ferrets were not found in any of the six areas.

Early Reward Programs

Throughout the 1970s, many States within the historical range of the black-footed ferret solicited sightings of ferrets. In 1974, Dr. Tim Clark, through an effort funded by the National Geographic Society and the National Academy of Sciences, solicited sightings from Wyoming and all States within the historical range of the black-footed ferret (Campbell, 1989). Clark went a step further by offering a $50 reward for a photograph or other information leading to the discovery of ferrets in the wild. "Wanted" posters (appendix, fig. A2) were widely distributed, and the reward was increased to $250 in 1980.

Other States, such as Oklahoma (Hassien, 1976) and New Mexico (Hubbard and Schmitt, 1983), had active publicity programs to solicit sighting reports of black-footed ferrets. The New Mexico Department of Game and Fish during 1978–81 and the New Mexico State Office of the Bureau of Land Management in 1982 conducted well-organized campaigns to solicit black-footed ferret sightings (Hubbard and Schmitt, 1983). The program was well publicized through posters, postcards, newspapers, magazines, and television. None of the 78 records produced was considered reliable evidence for the continued existence of black-footed ferrets in New Mexico (Hubbard and Schmitt, 1983).

Clark's $250 reward was paid to the finders of the Meeteetse, Wyo., ferret that led to the discovery of the last known extant population. Following that seminal event, biologists developed a program to locate ferrets in Montana by offering a monetary reward (Campbell, 1989). In 1983, Montana Fish, Wildlife and Parks and Biota Research and Consulting, Inc., developed a reporting system designed to standardize and assess ferret sightings, presenting criteria to evaluate each sighting and a protocol to follow if ferrets were discovered. The publicity resulted in 69 ferret reports by August 1986, but none resulted in locating and capturing a live black-footed ferret. In August 1986, Montana Fish, Wildlife and Parks initiated a new program soliciting ferret sightings but now offering a monetary reward (Flath, 1987). It included a mailer (appendix, fig. A3) describing the reward program and a standardized reporting form (appendix, fig. A3). A $5,000 reward for information leading to the discovery of a wild population of black-footed ferrets in Montana was offered by Wildlife Conservation International (a subsidiary of the New York Zoological Society). This program not only offered a significant reward but also made it the responsibility of the person submitting the sighting to include adequate information, limiting the need for follow-up on reports that were questionable. The reward program was aggressively advertised and included the distribution of "Wanted" posters (appendix, fig. A4) in post offices, public buildings, and businesses. The monetary reward program generated 66 additional responses (Campbell, 1989), but none led to the discovery of additional ferrets.

Recovery Activities at the National Ecology Research Center

In 1988, FWS approved a revised black-footed ferret recovery plan (U.S. Fish and Wildlife Service, 1988). The FWS's National Ecology Research Center (NERC; now the U.S. Geological Survey's Fort Collins Science Center) was responsible for completion of many of the revised recovery tasks outlined in the plan. One of these tasks was finding additional ferrets to bolster the depauperate genetic representation of ferrets in the captive breeding program. Biggins and Crete (1989), Hanebury and Biggins (1989), and Godbey and Biggins (1994) discussed FWS activities associated with finding ferrets under the new Black-footed Ferret Recovery

Plan. To locate additional ferrets, NERC expanded Montana's black-footed ferret reward program to other States and renewed black-footed ferret surveys on the best remaining ferret habitat.

National Reward Program

The Black-footed Ferret Interstate Coordinating Committee (ICC) was established in 1987 to improve communication and promote ferret recovery in 12 States, two Canadian Provinces, and the State of Chihuahua, Mexico. In 1987, the ICC identified the need for a national reward program and recommended a program similar to that used by Montana. In the fall of 1987, Wildlife Conservation International agreed to apply its $5,000 reward to any State within the former range of the black-footed ferret that wished to participate. States in the program had to be prepared to follow up on all reported sightings within a reasonable amount of time. Montana, Wyoming, Colorado, South Dakota, Utah, Nebraska, Oklahoma, Texas, and Arizona participated in the program. The Navajo Nation, encompassing a large area in both New Mexico and Arizona, also joined the effort. A new poster applicable to all States offering the $5,000 reward was prepared, and by February 1988, 10,000 copies were distributed. The revised posters (appendix, fig. A5) included a photo of a distinctive ferret-digging on snow and sketches of ferret tracks; to qualify for the reward, the observer needed to submit a photograph or information that resulted in verification of one or more live black-footed ferrets. To increase the quality and quantity of responses, Wildlife Conservation International agreed to increase the reward to $10,000 (appendix, fig. A6), effective March 3, 1989. Thousands of updated $10,000 reward posters were mailed to participating States.

New black-footed ferret sighting report forms were developed, incorporating the knowledge gathered from studying the Meeteetse population and experience gained from earlier ferret surveys in response to sighting reports. Ranking criteria and instructions were also developed. A sighting report was scored as highly probable, likely, fair, or unlikely. Such a classification was intended to limit follow-up investigations to the most probable sightings. This conservative approach addressed concerns about "probable" and "confirmed" sighting classifications used by Jobman and Anderson (1981a,b). They defined a probable sighting as one made by a qualified observer or a competent observer who was not positive about a sighting. A confirmed sighting was defined as one made by a competent and dependable observer who had no doubts that the animal seen was a black-footed ferret observed in or near suitable habitat (Jobman and Anderson, 1981a,b).

As part of the national reward program, an extensive effort was made to advertise the reward through all forms of local, statewide, and national media. The communications division of the Wyoming Game and Fish Department assisted NERC in producing audio and video public service announcements on the reward offer, which were sent to radio and television stations. Press releases describing summer and winter ferret behavior and sign, along with the posters, were distributed to the print media. Articles on the black-footed ferret reward program appeared in local and major newspapers and magazines. Major networks ran segments on programs such as *Missing: Reward* and NBC's *Today Show*, and special presentations such as the British Broadcasting Corporation's "Wildlife On One: Wanted Alive," which aired on *National Geographic Explorer*.

Responses to the reward program are difficult to quantify because each State handled incoming reports independently. Reports came directly to NERC or were forwarded from the receiving States. Although respondents provided descriptive photographs, drawings, and detailed characteristics, the photographs typically were of domestic ferrets (*Mustela putorius furo*) from both within and outside the black-footed ferret's historical range (e.g., California, Colorado, Florida, Kentucky, Nevada, Texas, and Utah), as well as photographs of long-tailed and bridled weasels (*Mustela frenata*), badgers, and prairie dogs. Photographs of black-footed ferrets were received from individuals in South Dakota and Alberta, Canada. Both of the photographs matched older photos taken by others, and both reports were judged to be hoaxes. The $10,000 reward offer was terminated on December 31, 1990.

Renewed Search Efforts

During the time of the national reward program, NERC formed black-footed ferret survey teams that were prepared to respond to valid sighting reports and to make one final effort to look for ferrets in suitable habitat. Between 1984 and 1988, six black-footed ferret sightings were reported in or around Waterton Lakes National Park in Alberta, Canada (Laing, 1988). Those reports were investigated in 1989 by Waterton Lakes National Park personnel, a local naturalist, NERC, and FWS personnel (Hanebury, 1989; Harvie, 1989; McGill, 1989). To lend credence to the reports, there were previous specimens or sighting records from Alberta and Saskatchewan (Russell, 1985; Anderson and others, 1986; Laing, 1987; Laing and Holroyd, 1989). In Canada, black-footed ferret surveys before this new effort were limited to those by Millson (1976), Laing (1987), and Laing and Holroyd (1989). Laing and Holroyd (1989) listed 15 recent sightings from 1967 to 1986 and surveyed all reported sites. No black-footed ferrets were confirmed by either the past efforts or the more recent efforts by NERC in and around Waterton Lakes National Park. Highly ranked reports on Navajo Nation lands in New Mexico were also investigated with negative results (Hanebury, 1988a). A brief search (26 person-hours) in the largest black-tailed prairie dog complex in North America, in Chihuahua, Mexico (Ceballos and others, 1993), did not detect any black-footed ferrets (Hanebury, 1988b), but there were 33 sightings of coyotes and 4 sightings of badgers. A partial tally of accessible data revealed 978 person-hours of spotlight searches conducted by NERC personnel in response to range-wide ferret sighting reports. The searches resulted in sightings of many other predators, including 187 coyotes, 193 badgers, and 17 long-tailed weasels, but the widely advertised $10,000 reward and subsequent investigations produced no proof of free-ranging ferrets.

In addition to responding to the sighting reports, NERC survey crews directed efforts to the locations that seemed most likely to harbor ferrets as determined by specimen records, clustered sighting reports, and information suggesting the presence of high-quality habitat (Jobman and Anderson, 1981b; Anderson and others, 1986; W. Jobman, written commun., 1984, 1992). These areas were located in South Dakota, Montana, and Wyoming. In the mid-1970s, when no remaining South Dakota ferret populations could be found, searches throughout the historical range of the black-footed ferret were undertaken by State resource agencies, private consultants, industry, university students, private citizens, and Federal agency biologists. Because no centralized repository for black-footed ferret survey data existed, it is impossible to quantify the hours devoted to spotlighting for ferrets, the area covered, or how many times the same area was searched through time.

Other evidence of a declining black-footed ferret population includes the number of ferret specimens obtained from poisoning, trapping, vehicle collisions, or other sources. Peak numbers occurred during the 1920s and 1930s (fig. 1), perhaps the period when the largest areas of prairie dog colonies were poisoned. Biggins and Schroeder (1988) speculated that this increase probably reflected increased attention given the species rather than a change in the population. No specimens were retrieved during the late 1970s and early 1980s. Although trapping probably decreased during that time, vehicular traffic and miles of roads increased. Cahalane (1954) reported that out of 42 sighting records from the period 1946–53, 17 ferrets were killed before or after the sighting. Four of those deaths were road kills between 1948 and 1953. During studies of the ferret population in south-central South Dakota in Mellette County, eight road-killed ferrets were documented in about 8 years (Hillman and Linder, 1973). There were no reported ferret road kills during the decade of the 1980s. It was not until 1994, after captive-bred black-footed ferrets were reintroduced to unoccupied habitat, that ferret specimens again began to be collected as road kills (fig. 1).

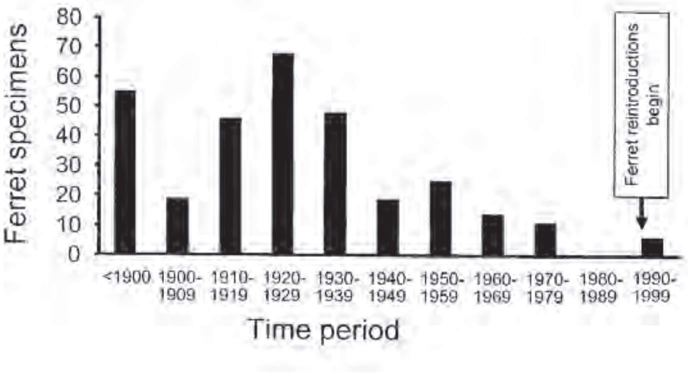


Figure 1. Number of black-footed ferret (*Mustela nigripes*) specimens collected by decade from Anderson and others (1986) and Clark (1989), including the decade after ferret reintroductions.

Summary

Since the decline of the last known ferret population in South Dakota, substantial effort has been devoted to identifying viable ferret habitat and locating any remaining isolated ferret populations. Survey techniques were developed and used as a reliable standard to find black-footed ferrets. Search efforts increased after the establishment of a policy for prairie dog precontrol surveys in 1965 and following implementation of the ESA in FWS field offices throughout the historical range of the ferret. None of the searches performed to implement recovery plan tasks, to comply with ESA section 7 consultation requirements (including pesticide registration), and to ensure compliance with the “take” prohibitions of section 9 of the ESA, nor heroic efforts by private individuals and conservation groups, have found any black-footed ferrets in the wild. At some locations, the lack of success in finding wild ferrets, combined with the desire by some agencies and organizations to expedite projects (e.g., prairie dog control, oil and gas development) in ferret habitat (i.e., prairie dog colonies), has resulted in requests for FWS to declare areas entirely “ferret free” (i.e., to “block-clear” the area from the need for preproject ferret searches) (Campbell and others, 1990). Today, requirements for preproject ferret surveys have been either officially eliminated or deemphasized in all of the 12 States composing the historical range of the black-footed ferret. The majority of the ferret range in South Dakota has been either block-cleared or exempted from the need for ferret surveys because of designation of experimental areas for ferret reintroduction through deliberative processes (South Dakota Department of Agriculture and South Dakota Department of Game, Fish and Parks, 2003). Other States with significant remaining areas of viable ferret habitat (active prairie dog colonies) have officially block-cleared habitat not considered valuable for ferret recovery (Colorado, R. Krueger, oral commun., 2005; Wyoming, M. Jennings, written commun., 2004). For the most part, North Dakota (B. Bicknell, oral commun., 2005), Nebraska (B. Harms, oral commun., 2005), Kansas (D. Mulhern, oral commun., 2005), Oklahoma (S. Harmon, oral commun., 2005), Utah (R. Chi, oral commun., 2005), and Texas (J. Hughs, oral commun., 2005) do not require preproject ferret surveys for section 7 consultation. New Mexico considers the black-footed ferret to be extirpated and therefore does not require preproject surveys (M. Murphy, oral commun., 2005).

Some organizations have promoted block-clearing as a strategy to improve public sentiment toward black-footed ferret recovery and prairie dog conservation (Patton and

Leachman, 1991). Further, the now widely held view that the probability of ferrets persisting in the wild is low, combined with the expense of conducting guideline-standard ferret searches, has caused FWS to relax section 7 consultation requirements (M. Lockhart, written commun., 2003) and propose that tasks relating to additional ferret searches be deemphasized in a second revision of the black-footed ferret recovery plan (U.S. Fish and Wildlife Service, 2004). A review of ferret survey needs is still in progress, however, and will be reflected in the final revised recovery plan.

Over 15 years ago, Lacy and Clark (1989) examined genetic variability in black-footed ferret populations and stated that it was unlikely that a long-term viable population of ferrets existed in the wild. We believe that the probability of finding ferrets that stem from noncaptive stock is already small and diminishes with each passing year. There are, however, several remaining considerations. With the reintroduction of over 1,900 captive-raised black-footed ferrets and with much recruitment of wild-born kits since 1991, the possibility of newly established populations in the wild will increase. The example of the remarkable persistence of ferrets in the disease-prone, vast, but fragmented habitat of Shirley Basin, Wyo. (Grenier and others, 2004), gives us hope that free-ranging ferrets will persist in other States as reintroductions continue. In addition to the need to monitor reestablished ferret populations, there will be a continued need for improved monitoring methodologies and searches to locate future populations established by dispersing young.

References Cited

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Anderson, S.H., and Inkley, D.B., eds., 1985, Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 1.1–33.12.

Berryman, J.H., and Johnson, N.C., 1973, Ferret and prairie dog programs on public lands—a perspective and some facts, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 109–125.

Biggins, D., 1983, Movements and activity patterns of radio-tagged black-footed ferrets: U.S. Fish and Wildlife Service Summary Report, 48 p.

Biggins, D.E., and Crete, R.A., 1989, Black-footed ferret recovery, *in* Bjugstad, A.J., Uresk, D.W., and Hamre, R.H., technical coordinators, Ninth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-171, p. 59–63.

Biggins, D.E., and Engeman, R.E., 1986, Aerial survey for black-footed ferret sign in snow, *in* Abstracts of contributed papers, 13th International Biometrics Conference, Seattle, Wash.: Washington, D.C., International Biometrics Society, p. 7.2.

Biggins, D.E., and Fagerstone, K.A., 1983, Black-footed ferret research, Meeteetse, Wyoming: Fort Collins, Colo., U.S. Fish and Wildlife Service, Denver Wildlife Research Center, 5 p.

Biggins, D.E., and Schroeder, M.H., 1988, Historical and present status of the black-footed ferret, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 93–97.

Biggins, D.E., Schroeder, M.H., Forrest, S.C., and Richardson, L., 1986, Activity of radio-tagged black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 135–140.

Brussard, P.F., and Gilpin, M.E., 1989, Demographic and genetic problems of small populations, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 37–48.

Cada, J.D., 1985, Montana's role in ferret management and handling of ferret sightings, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 14.1–14.7.

Cahalane, V.H., 1954, Status of the black-footed ferret: Journal of Mammalogy, v. 35, p. 418–424.

Campbell, T.M., III, 1989, Prairie dog colony location surveys and black-footed ferret searches in Montana, *in* Clark, T.W., Hinckley, D., and Rich, T., eds., The prairie dog ecosystem—managing for biological diversity: Billings, Montana BLM Wildlife Technical Bulletin No. 2., p. 1–12.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Campbell, T.M., III, Crete, R., and Leachman, R., 1990, Strategy for block clearance of prairie dog colonies and complexes (draft): Denver, Colo., U.S. Fish and Wildlife Service, 14 p.

Carpenter, J.W., and Hillman, C.N., 1978, Husbandry, reproduction, and veterinary care of captive ferrets: American Association of Zoo Veterinarians, Annual Proceedings, p. 36–47.

Ceballos, G., Mellink, E., and Hanebury, L.R., 1993, Distribution and conservation status of prairie dogs *Cynomys mexicanus* and *Cynomys ludovicianus* in Mexico: Biological Conservation, v. 63, p. 105–112.

Clark, T.W., 1973, Prairie dogs and black-footed ferrets in Wyoming, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 88–101.

Clark, T.W., 1978, Current status of the black-footed ferret in Wyoming: Journal of Wildlife Management, v. 42, p. 128–134.

Clark, T.W., 1980, A listing of reports of black-footed ferrets in Wyoming (1851–1977): Northwest Science, v. 54, p. 47–54.

Clark, T.W., 1985, Black-footed ferret studies in Wyoming: National Geographic Society Research Reports, v. 18, p. 223–231.

Clark, T.W., 1989, Conservation biology of the black-footed ferret, *Mustela nigripes*: Philadelphia, Wildlife Preservation Trust International, Special Scientific Report No. 3, 175 p.

Clark, T.W., and Campbell, T.M., III, 1981a, Suggested guidelines for black-footed ferret surveys: Jackson, Wyo., Biota Research and Consulting, Inc., 7 p.

Clark, T.W., and Campbell, T.M., III, 1981b, Additional black-footed ferret (*Mustela nigripes*) reports from Wyoming: Great Basin Naturalist, v. 41, p. 360–361.

Clark, T.W., and Campbell, T.M., III, 1983, A small carnivore survey technique: Great Basin Naturalist, v. 43, p. 438–440.

Clark, T.W., Campbell, T.M., III, Schroeder, M.H., and Richardson, L., 1984a, Handbook of methods for locating black-footed ferrets: Cheyenne, Wyoming BLM Technical Bulletin No. 1, 55 p.

Clark, T.W., Campbell, T.M., III, Schroeder, M.H., and Richardson, L., 1988, Handbook of methods for locating black-footed ferrets: Cheyenne, Wyoming BLM Technical Bulletin No. 1, 61 p.

Clark, T.W., Richardson, L., Casey, D., Campbell, T.M., III, and Forrest, S.C., 1984b, Seasonality of black-footed ferret diggings and prairie dog burrow plugging: Journal of Wildlife Management, v. 48, p. 1441–1444.

Clark, T.W., Richardson, L., Forrest, S.C., Casey, D.E., and Campbell, T.M., III, 1986, Descriptive ethology and activity patterns of black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 115–134.

Conway, M.C., and Dean, E.E., 1979, Endangered species: dog training for black-footed ferret detection: New Mexico Department of Game and Fish, project no. N.M. E-001-R-01.

Crete, R., 1985, Current activities of the U.S. Fish and Wildlife Service in black-footed ferret recovery management, *in* Anderson, S.H., and Inkley, D.B, eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 15.1–15.6.

Fagerstone, K.A., and Biggins, D.E., 1986, Summary of black-footed ferret and related research conducted by the Denver Wildlife Research Center, 1981–1985: Denver, Colo., U.S. Fish and Wildlife Service, Denver Wildlife Research Center, 31 p.

Flath, D., 1987, Wanted: the masked stranger: Montana Outdoors, v. 18, p. 18–22.

Fortenbery, D.K., 1972, Characteristics of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Resource Publication 109, 8 p.

Godbey, J., and Biggins, D., 1994, Recovery of the black-footed ferret—looking back, looking forward: Endangered Species Technical Bulletin, v. 19, p. 10–13.

Grenier, M., Van Fleet, L., and Oakleaf, B., 2004, Spotlighting for free ranging black-footed ferrets in the Shirley Basin/Medicine Bow Management Area, Wyoming, *in* Cerovski, A.O., ed., Threatened, endangered and nongame bird and mammal investigations: Cheyenne, Wyoming Game and Fish Department, p. 19–35.

Grode, M.R., 1985, The black-footed ferret in Colorado, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 17.1–17.4.

Grondahl, C.R., 1973, Status of the black-tailed prairie dog and black-footed ferret in North Dakota, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 51–60.

Hammer, D.A., 1985, The handling of black-footed ferret sighting reports in Wyoming, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 18.1–18.4.

Hammer, D.A., and Anderson, S.H., 1985, Using scent attractants as a technique to locate black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 26.1–26.12.

Hanebury, L.R., 1988a, Black-footed ferret surveys on Navajo Tribal Lands: Fort Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 14 p.

Hanebury, L.R., 1988b, Black-tailed prairie dog and black-footed ferret investigations in Chihuahua, Mexico: Fort

Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 27 p.

Hanebury, L.R., 1989, Black-footed ferret investigations in Canada—return to Waterton Lakes National Park, Waterton Lakes, Alberta, February 20–23, 1989: Fort Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 4 p.

Hanebury, L.R., and Biggins, D., 1989, Black-footed ferret recovery update: Endangered Species Technical Bulletin, v. 14, p. 10.

Hanson, R., 1988, A chronology of prairie dog control operations and related developments in South Dakota, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 121–122.

Hanson, R., 1993, Control of prairie dogs and related developments in South Dakota, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 5–7.

Harvie, W., 1989, The black-footed ferret frenzy—wildlife lovers search Waterton Park for the elusive species: Alberta Report, May 8, 1989, p. 24.

Hasenyager, R., 1985, Utah's ferret program—past, present and future?, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 19.1–19.2.

Hassien, F.D., 1976, A search for black-footed ferrets in the Oklahoma Panhandle and adjacent areas and an ecological study of the black-tailed prairie dog in Texas County, Oklahoma: Stillwater, Oklahoma State University, M.S. thesis, 111 p.

Henderson, F.R., 1969, Wanted—black-footed ferret: Manhattan, Kansas State University, Cooperative Extension Service, 8 p.

Henderson, F.R., and Little, R.J., 1973, Status of the black-footed ferret and black-tailed prairie dog in Kansas, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 34–44.

Henderson, F.R., Springer, P.F., and Adrian, R., 1969, The black-footed ferret in South Dakota: Pierre, South Dakota Department of Game, Fish, and Parks, Technical Bulletin 4, 37 p.

Hillman, C.N., 1968a, Life history and ecology of the black-footed ferret in the wild: Brookings, South Dakota State University, M.S. thesis, 29 p.

Hillman, C.N., 1968b, Field observations of black-footed ferrets in South Dakota: Transactions of the North American Wildlife and Natural Resources Conference, v. 33, p. 433–443.

Hillman, C.N., and Linder, R.L., 1973, The black-footed ferret, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 10–23.

Hubbard, J.P., and Schmitt, C.G., 1983, The black-footed ferret in New Mexico: Santa Fe, New Mexico Game and Fish Department, 118 p.

Jobman, W.G., and Anderson, M.E., 1981a, Potential present range of the black-footed ferret as of January 1, 1981: Pierre, S. Dak., U.S. Fish and Wildlife Service, 64 p.

Jobman, W.G., and Anderson, M.E., 1981b, Current black-footed ferret range as indicated by questionnaire survey: Pierre, S. Dak., U.S. Fish and Wildlife Service, 32 p.

Jobman, W.G., and Anderson, M.E., 1985, Legal status and required action ferret research and management, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 2.1–2.8.

Johnson, M.K., Clark, T.W., Schroeder, M.H., and Richardson, L., 1986, Fecal bile acids of black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 141–144.

Lacy, R.C., and Clark, T.W., 1989, Genetic variability in black-footed ferret populations—past, present, and future, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 83–103.

Laing, R.I., 1987, The reestablishment of the black-footed ferret to the Canadian prairie, *in* Holroyd, G.L., McGillivray, W.B., Stepney, P.H.R., Ealey, D.M., Trottier, G.C., and Eberhart, K.E., eds., Proceedings of the workshop on endangered species in the Prairie Provinces, January 24–26, 1986: Edmonton, Provincial Museum of Alberta Natural History, Occasional Paper No. 9, p. 293–297.

Laing, R.I., 1988, Black-footed ferret habitat mapping and verification in Waterton Lakes National Park, 1988: Report to Environment Canada, Canadian Park Service, 19 p.

Laing, R.I., and Holroyd, G.L., 1989, The status of the black-footed ferret in Canada: Blue Jay, v. 47, p. 121–125.

Lengkeek, D., 1985, Black-footed ferret program in South Dakota, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 21.1–21.4.

Lewis, J.C., 1973, Additional records of black-footed ferrets in Oklahoma: Southwestern Naturalist, v. 18, p. 350.

Lewis, J.C., and Hassien, F., 1973, Status of prairie dogs and surveys for black-footed ferrets in Oklahoma, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 60–75.

Linder, R.L., and Hillman, C.N., preparers, 1973, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, 208 p.

Lindzey, F., and Marinari, P.E., 1992, Spotlighting for black-footed ferrets: U.S. Fish and Wildlife Service, Research Information Bulletin No. 74, 2 p.

Locke, R.A., 1973, Status of the black-footed ferret and black-tailed prairie dog in Nebraska, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 44–47.

Marinari, P.E., 1992, Detectability of black-footed ferrets using spotlighting: Laramie, University of Wyoming, M.S. thesis, 126 p.

Martin, S.J., 1983, Additional records of black-footed ferrets in Wyoming: Southwestern Naturalist, v. 28, p. 95.

Martin, S.J., and Schroeder, M.H., 1979, Black-footed ferret surveys on seven coal occurrence areas in southwestern and southcentral Wyoming (June to September 1978): Cheyenne, Wyo., final report to the Bureau of Land Management, 37 p.

Martin, S.J., and Schroeder, M.H., 1980, Black-footed ferret surveys on seven coal occurrence areas in Wyoming (February to September 1979): Fort Collins, Colo., U.S. Fish Wildlife Service and Bureau of Land Management, Ferret Report No. 2, 34 p.

Matchett, R., and Smith, D., 2001, Use of dogs for black-footed ferret presence detection—progress report: Lewistown, Mont., Charles M. Russell National Wildlife Refuge, 4 p.

McGill, R.J., 1989, Black-footed ferret—final report for Waterton Lakes National Park: Waterton Lakes, Alberta, Environment Canada, Canadian Park Service, 6 p.

Millson, R., 1976, The black-footed ferret in the proposed Grasslands National Park: University of Calgary, Alberta, Canada, M.S. thesis, 107 p.

Morkill, A., 1987, Black-footed ferret surveys—statewide, completion report, April 15, 1986 to April 14, 1987, *in* Oakleaf, B., Belitsky, D., and Ritter, S., eds., Endangered and nongame bird and mammal investigations, annual completion report: Lander, Wyoming Game and Fish Department, Nongame Program, Biological Services Section, p. 59–68.

Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., 1993, Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, 97 p.

Patton, G., and Leachman, R., 1991, Black-footed ferret habitat evaluation and search project in Northeast Colorado. Final report: Grand Junction, Colo., U.S. Fish and Wildlife Service, 56 p.

Reindl, S.A., 2004, Efficacy of scent dogs in detecting black-footed ferrets (*Mustela nigripes*) at a reintroduction site in South Dakota: Brookings, South Dakota State University, M.S. Thesis, 60 p.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1985, Snow-tracking as a method to search for and study the black-footed ferret, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 25.1–25.11.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming: American Midland Naturalist, v. 117, p. 225–239.

Russell, R.H., 1985, The black-footed ferret in Canada, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 20.1–20.2.

Schroeder, M., 1988, Endangered species considerations in prairie dog management, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 123–124.

Schroeder, M.H., 1985, U.S. Fish and Wildlife Service guidelines for black-footed ferret surveys, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 27.1–27.5.

Schroeder, M.H., and Martin, S., 1982, Search for the black-footed ferret succeeds: Wyoming Wildlife, v. 46, p. 8–9.

Sheets, R.G., 1970, Ecology of the black-footed ferret and the black-tailed prairie dog: Brookings, South Dakota State University, M.S. thesis, 51 p.

Smith, D.W., Hammer, D.A., Schroeder, M.H., and Martin, S.J., 1982, Black-footed ferret surveys on coal occurrence areas in southcentral Wyoming, June–September, 1981. Final report: Fort Collins, Colo., U.S. Fish and Wildlife Service, Denver Wildlife Research Center, 43 p.

South Dakota Department of Agriculture and South Dakota Department of Game, Fish and Parks, 2003, An evaluation of the block clearance process in South Dakota: Pierre, S. Dak., 17 p.

Southwest Research Institute, 1979, Training of dogs to detect black-footed ferrets: San Antonio, Tex., Southwest Research Institute, project report no. 14-5331, 7 p.

U.S. Environmental Protection Agency, 1987, Strychnine; intent to cancel; partial withdrawal of prior cancellation notice: Federal Register, v. 52, p. 6762–6765.

U.S. Fish and Wildlife Service, 1978, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 145 p.

U.S. Fish and Wildlife Service, 1986, Black-footed ferret survey guidelines for compliance with the Endangered Species Act: Denver, Colo., and Albuquerque, N. Mex., U.S. Fish and Wildlife Service, 17 p.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

U.S. Fish and Wildlife Service, 1989, Black-footed ferret search activities, northwest Colorado and Northeast Utah: Golden, Colo., U.S. Fish and Wildlife Service, 49 p.

U.S. Fish and Wildlife Service, 1991, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in southeastern Wyoming: Federal Register, v. 56, p. 23830–23842.

U.S. Fish and Wildlife Service, 1992, Reintroduction of the black-footed ferret *Mustela nigripes*: Fort Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 44 p.

U.S. Fish and Wildlife Service, 1993, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in north-central Montana: Federal Register, v. 58, p. 19220–19231.

U.S. Fish and Wildlife Service, 1994, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in south-western South Dakota: Federal Register, v. 59, p. 42682–42694.

U.S. Fish and Wildlife Service, 1996, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in Aubrey Valley, Arizona: Federal Register, v. 61, p. 11320–11336.

U.S. Fish and Wildlife Service, 1998, Endangered and threatened wildlife and plants—proposed establishment of a nonessential population of black-footed ferrets in northwestern Colorado and northeastern Utah: Federal Register, v. 63, p. 52824–52841.

U.S. Fish and Wildlife Service, 2004, Draft black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 136 p.

Wyoming Game and Fish Department, 1992, Black-footed ferret reintroduction in Shirley Basin, Wyoming—1991 annual completion report: Cheyenne, Wyoming Game and Fish Department, 256 p.

Wyoming Game and Fish Department, 1993, Black-footed ferret reintroduction in Shirley Basin, Wyoming—1992 annual completion report: Cheyenne, Wyoming Game and Fish Department, 244 p.

Wyoming Game and Fish Department, 1994, Black-footed ferret reintroduction in Shirley Basin, Wyoming—1993 annual completion report: Cheyenne, Wyoming Game and Fish Department, 94 p.

Wyoming Game and Fish Department, 1995, Black-footed ferret reintroduction in Shirley Basin, Wyoming—1994 annual completion report: Cheyenne, Wyoming Game and Fish Department, 59 p.

Appendix. Posters Used To Solicit Reports of Black-footed Ferret Sightings

WANTED ALIVE
Black Footed Ferrets
and Their Location

Photo—F. Robert Henderson

Size: About 2 feet long including the tail.
Identifying Markings: Black face-mask, black-tipped tail, black feet, body color is yellow-tan.
Habitat: Usually prairie dog towns or near them. May be seen elsewhere when moving between prairie dog towns, during searches for food and during breeding season.
Abundance: One of rarest mammals in North America.

PLEASE, report! (See contact at bottom of poster)

DON'T BE CONFUSED BY THESE ANIMALS THAT LOOK LIKE THE BLACK-FOOTED FERRET

Photo—F. Robert Henderson

European Ferret

Size: About the same as the black-footed ferret.
Identifying Markings: Similar to those of the black-footed ferret, **except,** nose more pointed, more black on tail and the fur is more bushy to give a heavier body appearance. Body color usually appears darker, because of dark-colored guard hairs. Feet **are** black.
Habitat and Abundance: Common laboratory animal and sold in pet shops. Often released to the wild by owners.

Photo—Jon Farrar

Long-Tailed Weasel

Size: About one-half the size of a black-footed ferret.
Identifying Markings: Yellowish-white underparts and black-tipped tail. Body color is reddish-brown. Winter color is white except black-tipped tail. Feet **not** black.
Habitat and Abundance: Can be found on most land habitats where prey species available, and often near water.

Bridled Weasel

Size: About one-half the size of a black-footed ferret.
Identifying Markings: Same as long-tailed weasel only has black face-mask. Feet **not** black.
Habitat and Abundance: Similar to long-tailed weasel. Mostly occurs in Southwestern U.S.

Photo—Ernie Peck

Cooperative Extension Service
Kansas State University
and
The U.S. Department of the Interior
Fish and Wildlife Service

All educational programs and materials are available without discrimination on the basis of race, color, national origin, sex, or handicap.

PLEASE REPORT TO:

Lou Hanebury - National Ecology Center, USFWS
1300 Blue Spruce Drive
Fort Collins, CO 80524
(303) 226-9460 Night (303) 224-2849

Figure A1. The first poster used to solicit information about locations of black-footed ferrets (*Mustela nigripes*) (original poster was in color).

WANTED

DO
NOT
KILL
OR
TRAP

DO
NOT
KILL
OR
TRAP

$50 REWARD

for Photograph & Information

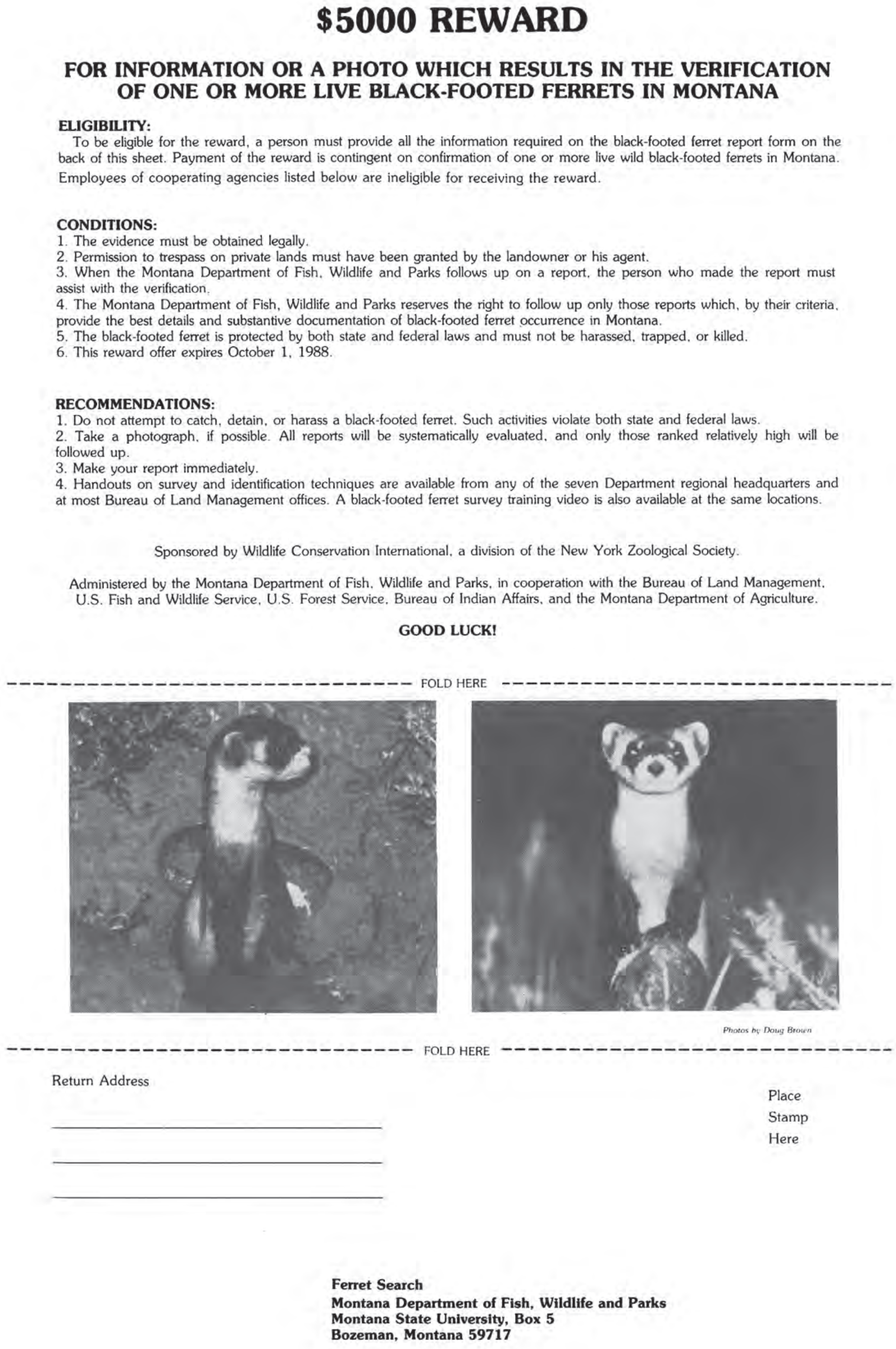
REWARD CONDITIONS: The ferret is an endangered species and is protected by very stringent federal and state laws. The reward WILL NOT be paid for any ferret caught in traps or killed by the finder. The reward will be given to the FIRST person providing information leading to the discovery and verification of the existence of black-footed ferrets (*Mustela nigripes*) in Wyoming. Skins and skeletons of ferrets struck accidently by cars and found along roads, reports of ferrets seen or photographs taken in an area where a representative of the "Ferret Search" project subsequently observes a ferret will qualify for the reward. A few ferrets have been seen in most parts of Wyoming in recent years. Ferrets eat prairie dogs and are usually found on or near prairie dog towns.

IDENTIFYING CHARACTERISTICS: The ferret is the size of a medium sized mink, about 18 inches long and 2.5 pounds. Unique features are black face mask and black feet. Do not confuse it with long-tailed weasels (no mask or black feet).

CONTACT: Tim W. Clark, Ferret Search, Box 1330, Jackson, Wyoming 83001; Telephone: 307-733-4806 as soon as possible after the sighting.

"Ferret Search" supported by National Geographic Society and The National Academy of Sciences. Reward offer expires 1 November, 1975.

Figure A2. A 1974 poster distributed by Tim Clark, offering a $50 reward for information leading to discovery of black-footed ferrets (*Mustela nigripes*).



$5000 REWARD

FOR INFORMATION OR A PHOTO WHICH RESULTS IN THE VERIFICATION OF ONE OR MORE LIVE BLACK-FOOTED FERRETS IN MONTANA

ELIGIBILITY:

To be eligible for the reward, a person must provide all the information required on the black-footed ferret report form on the back of this sheet. Payment of the reward is contingent on confirmation of one or more live wild black-footed ferrets in Montana. Employees of cooperating agencies listed below are ineligible for receiving the reward.

CONDITIONS:

1. The evidence must be obtained legally.
2. Permission to trespass on private lands must have been granted by the landowner or his agent.
3. When the Montana Department of Fish, Wildlife and Parks follows up on a report, the person who made the report must assist with the verification.
4. The Montana Department of Fish, Wildlife and Parks reserves the right to follow up only those reports which, by their criteria, provide the best details and substantive documentation of black-footed ferret occurrence in Montana.
5. The black-footed ferret is protected by both state and federal laws and must not be harassed, trapped, or killed.
6. This reward offer expires October 1, 1988.

RECOMMENDATIONS:

1. Do not attempt to catch, detain, or harass a black-footed ferret. Such activities violate both state and federal laws.
2. Take a photograph, if possible. All reports will be systematically evaluated, and only those ranked relatively high will be followed up.
3. Make your report immediately.
4. Handouts on survey and identification techniques are available from any of the seven Department regional headquarters and at most Bureau of Land Management offices. A black-footed ferret survey training video is also available at the same locations.

Sponsored by Wildlife Conservation International, a division of the New York Zoological Society.

Administered by the Montana Department of Fish, Wildlife and Parks, in cooperation with the Bureau of Land Management, U.S. Fish and Wildlife Service, U.S. Forest Service, Bureau of Indian Affairs, and the Montana Department of Agriculture.

GOOD LUCK!

FOLD HERE

Photos by Doug Brown

FOLD HERE

Return Address

____

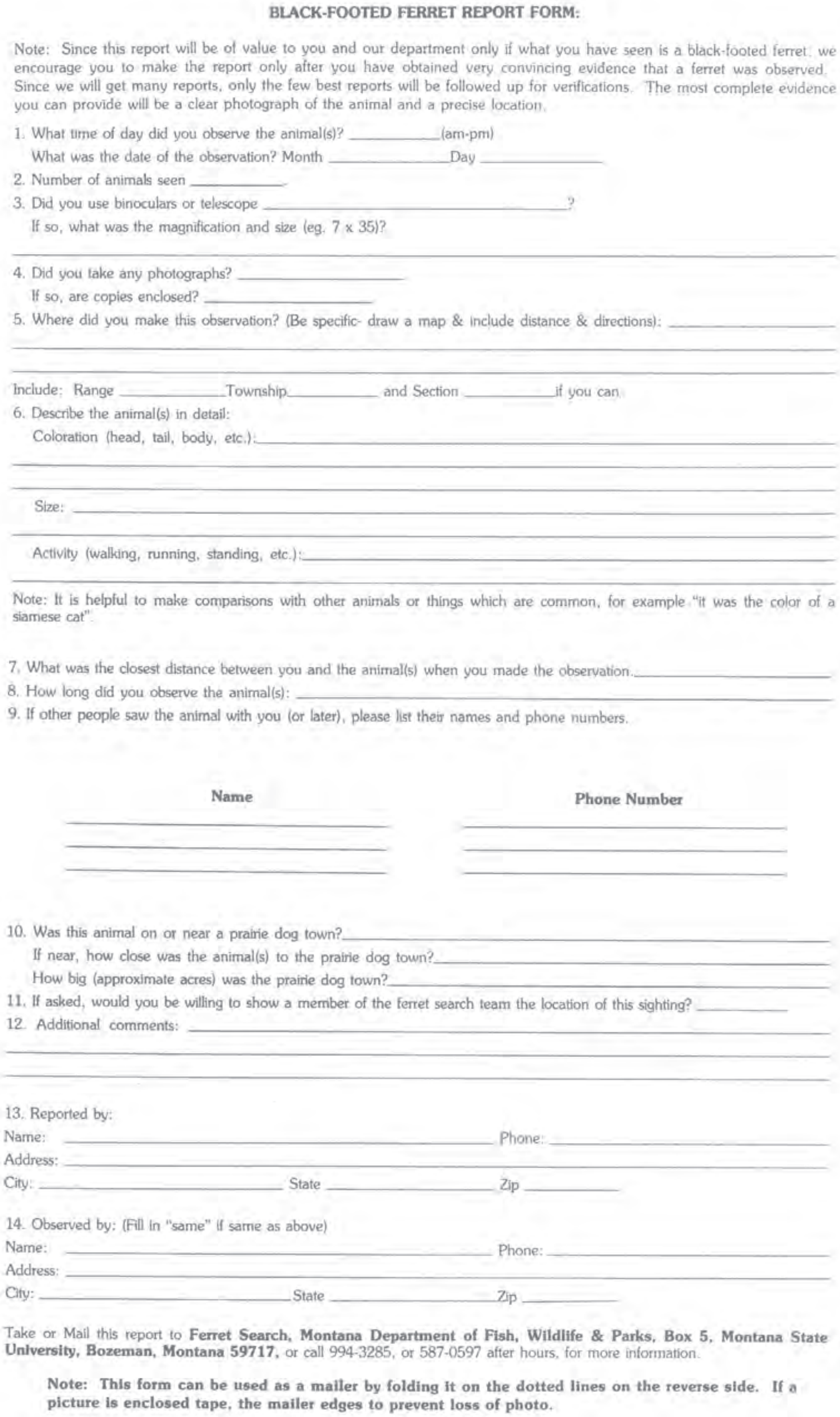
____

____

Place
Stamp
Here

Ferret Search
Montana Department of Fish, Wildlife and Parks
Montana State University, Box 5
Bozeman, Montana 59717

Figure A3. A pamphlet and report form, distributed in Montana starting in 1983, advertising a $5,000 reward for a verified black-footed ferret (*Mustela nigripes*) sighting.



BLACK-FOOTED FERRET REPORT FORM:

Note: Since this report will be of value to you and our department only if what you have seen is a black-footed ferret, we encourage you to make the report only after you have obtained very convincing evidence that a ferret was observed. Since we will get many reports, only the few best reports will be followed up for verifications. The most complete evidence you can provide will be a clear photograph of the animal and a precise location.

1. What time of day did you observe the animal(s)? ____________(am-pm)
   What was the date of the observation? Month ______________Day ______________
2. Number of animals seen ____________.
3. Did you use binoculars or telescope ____________________________________?
   If so, what was the magnification and size (eg. 7 x 35)?
4. Did you take any photographs? ____________________
   If so, are copies enclosed? ____________________
5. Where did you make this observation? (Be specific- draw a map & include distance & directions): ____________________

Include: Range ____________Township____________ and Section ____________if you can.

6. Describe the animal(s) in detail:
   Coloration (head, tail, body, etc.):____________________
   Size: ____________________
   Activity (walking, running, standing, etc.):____________________

Note: It is helpful to make comparisons with other animals or things which are common, for example "it was the color of a siamese cat".

7. What was the closest distance between you and the animal(s) when you made the observation.____________________
8. How long did you observe the animal(s): ____________________
9. If other people saw the animal with you (or later), please list their names and phone numbers.

Name	Phone Number

10. Was this animal on or near a prairie dog town?____________________
    If near, how close was the animal(s) to the prairie dog town?____________________
    How big (approximate acres) was the prairie dog town?____________________
11. If asked, would you be willing to show a member of the ferret search team the location of this sighting? ____________
12. Additional comments: ____________________

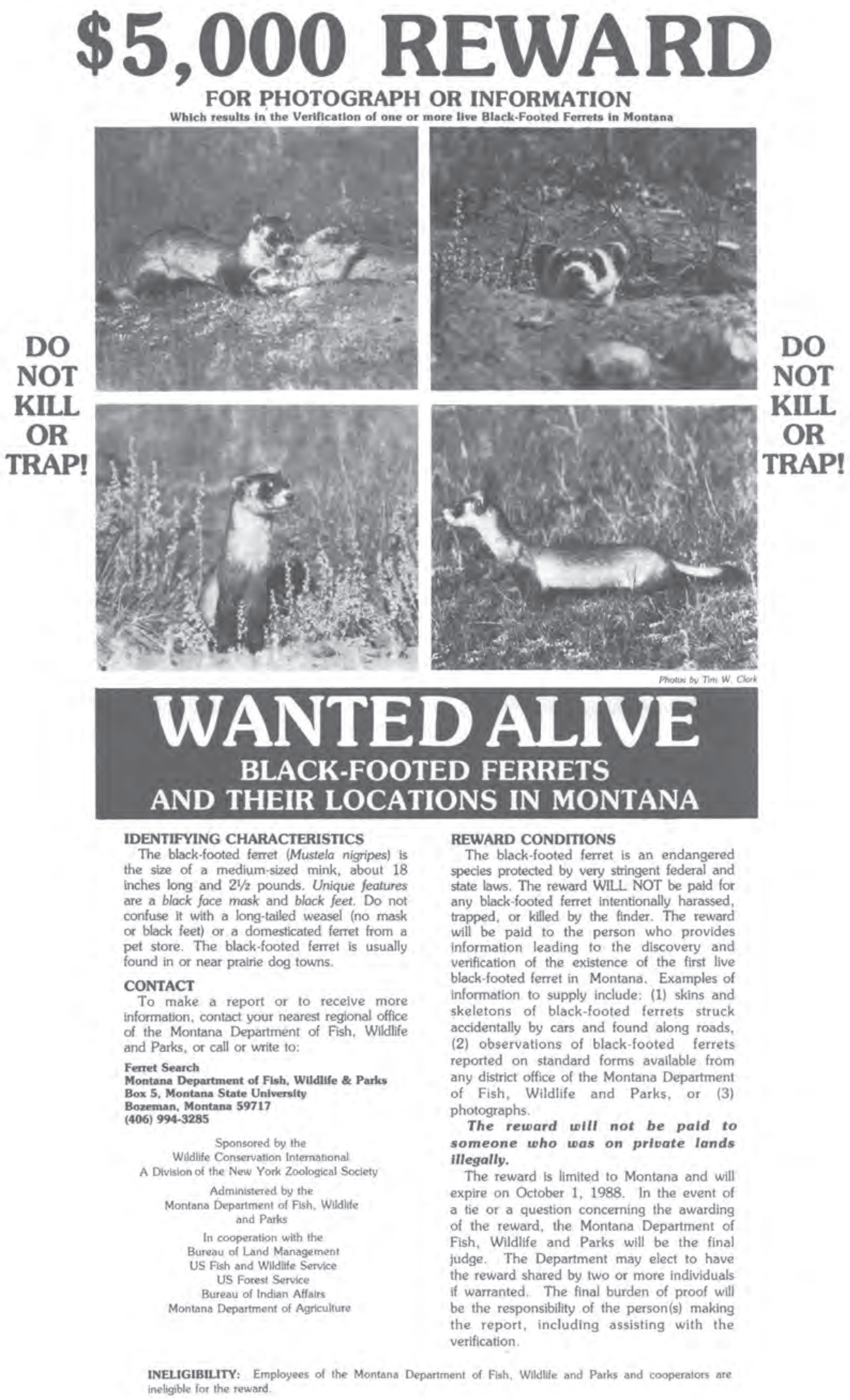
13. Reported by:
Name: ____________________ Phone: ____________________
Address: ____________________
City: ____________________ State ____________________ Zip ____________

14. Observed by: (Fill in "same" if same as above)
Name: ____________________ Phone: ____________________
Address: ____________________
City: ____________________State ____________________Zip ____________

Take or Mail this report to **Ferret Search, Montana Department of Fish, Wildlife & Parks, Box 5, Montana State University, Bozeman, Montana 59717,** or call 994-3285, or 587-0597 after hours, for more information.

Note: This form can be used as a mailer by folding it on the dotted lines on the reverse side. If a picture is enclosed tape, the mailer edges to prevent loss of photo.

Figure A3. A pamphlet and report form, distributed in Montana starting in 1983, advertising a $5,000 reward for a verified black-footed ferret (*Mustela nigripes*) sighting.—Concluded.



$5,000 REWARD

FOR PHOTOGRAPH OR INFORMATION

Which results in the Verification of one or more live Black-Footed Ferrets in Montana

DO
NOT
KILL
OR
TRAP!

DO
NOT
KILL
OR
TRAP!

Photos by Tim W. Clark

WANTED ALIVE

BLACK-FOOTED FERRETS AND THEIR LOCATIONS IN MONTANA

IDENTIFYING CHARACTERISTICS

The black-footed ferret (*Mustela nigripes*) is the size of a medium-sized mink, about 18 inches long and 2½ pounds. *Unique features* are a *black face mask* and *black feet.* Do not confuse it with a long-tailed weasel (no mask or black feet) or a domesticated ferret from a pet store. The black-footed ferret is usually found in or near prairie dog towns.

CONTACT

To make a report or to receive more information, contact your nearest regional office of the Montana Department of Fish, Wildlife and Parks, or call or write to:

Ferret Search
Montana Department of Fish, Wildlife & Parks
Box 5, Montana State University
Bozeman, Montana 59717
(406) 994-3285

Sponsored by the
Wildlife Conservation International
A Division of the New York Zoological Society

Administered by the
Montana Department of Fish, Wildlife
and Parks

In cooperation with the
Bureau of Land Management
US Fish and Wildlife Service
US Forest Service
Bureau of Indian Affairs
Montana Department of Agriculture

REWARD CONDITIONS

The black-footed ferret is an endangered species protected by very stringent federal and state laws. The reward WILL NOT be paid for any black-footed ferret intentionally harassed, trapped, or killed by the finder. The reward will be paid to the person who provides information leading to the discovery and verification of the existence of the first live black-footed ferret in Montana. Examples of information to supply include: (1) skins and skeletons of black-footed ferrets struck accidentally by cars and found along roads, (2) observations of black-footed ferrets reported on standard forms available from any district office of the Montana Department of Fish, Wildlife and Parks, or (3) photographs.

The reward will not be paid to someone who was on private lands illegally.

The reward is limited to Montana and will expire on October 1, 1988. In the event of a tie or a question concerning the awarding of the reward, the Montana Department of Fish, Wildlife and Parks will be the final judge. The Department may elect to have the reward shared by two or more individuals if warranted. The final burden of proof will be the responsibility of the person(s) making the report, including assisting with the verification.

INELIGIBILITY: Employees of the Montana Department of Fish, Wildlife and Parks and cooperators are ineligible for the reward.

Figure A4. A poster used to further advertise the Montana $5,000 reward supported by the New York Zoological Society, distributed in 1986–87.

$5,000 REWARD

FOR PHOTOGRAPH OR INFORMATION WHICH RESULTS IN VERIFICATION OF ONE OR MORE LIVE BLACK-FOOTED FERRETS

DO NOT KILL OR TRAP

Upper two black-footed ferrets by Dean Biggins. Ferret with prairie dog kill by Tim Clark. Ferret digging by Louise Forrest.

WANTED ALIVE

Black-footed ferrets and their locations

CHARACTERISTICS

The black-footed ferret *(Mustela nigripes)*, a nocturnal predator, is the size of a medium-sized mink, about 18 inches long and 2½ pounds. **Unique features are a black face mask and black legs.** Do not confuse it with a long-tailed weasel, a smaller animal without black legs. The domestic ferret sold in pet stores is not a black-footed ferret. The black-footed ferret is usually found in or near prairie dog towns.

DIGGINGS

Diggings can be evidence of ferret presence if they are found in winter and prairie dogs have been inactive. Black-footed ferret diggings are deposits of loose soil pulled from prairie dog size burrows (about 4-inches wide) and left on the surface of the ground or snow (see photograph). A digging should be reported if:

(1) it is deposited on snow and is accompanied by "twin print" type tracks (see illustration in margins)

OR

(2) it is deposited on the ground, is more than 3 feet long, is less than 12 inches wide, and has a trough or furrow-like depression centered along its length.

REWARD CONDITIONS

The black-footed ferret is an endangered species protected by very stringent federal and state laws. The reward WILL NOT be paid for any black-footed ferret intentionally harassed, trapped, or killed by the finder. The reward will be paid to the first person who provides information leading to the discovery and verification of the first live black-footed ferret in each state. Examples of information to supply include: (1) skins and skeletons of black-footed ferrets struck accidentally by cars and found along roads, (2) photographs of ferrets or ferret diggings, or (3) observations of black-footed ferrets or ferret diggings.

The reward will not be paid to someone who was on private lands illegally.

The reward offer is limited to participating states. In the event of a tie or a question concerning the awarding of the reward, the U.S. Fish and Wildlife Service will be the final judge. The Service may elect to have the reward shared by two or more individuals if warranted. The final burden of proof, including assisting with the verification, will be the responsibility of the person making the report. The reward offer is valid from September 1, 1987 through September 31, 1989.

CONTACT To make a report or to receive more information on how to find black-footed ferrets, call or write to:

Lou Hanebury - National Ecology Center, USFWS
1300 Blue Spruce Drive
Fort Collins, CO 80524
(303) 226-9460 Night (303) 224-2849

INELIGIBILITY Employees (and their relatives) of the U.S. Fish and Wildlife Service, State Conservation Agencies, and cooperators are ineligible for the reward.

Reward sponsored by the Wildlife Conservation International, a division of the New York Zoological Society.

Figure A5. The poster used to advertise the New York Zoological Society's $5,000 reward after the reward was offered nationally during 1987–89.

$10,000 REWARD

FOR PHOTOGRAPH OR INFORMATION WHICH RESULTS IN VERIFICATION OF ONE OR MORE LIVE BLACK-FOOTED FERRETS

DO NOT KILL OR TRAP

Upper two black-footed ferrets by Dean Biggins. Ferret with prairie dog kill by Tim Clark. Ferret digging by Louise Forrest.

WANTED ALIVE

Black-footed ferrets and their locations

CHARACTERISTICS

The black-footed ferret *(Mustela nigripes)*, a nocturnal predator, is the size of a medium-sized mink, about 18 inches long and 2½ pounds. **Unique features are a black face mask and black legs.** Do not confuse it with a long-tailed weasel, a smaller animal without black legs. The domestic ferret sold in pet stores is not a black-footed ferret. The black-footed ferret is usually found in or near prairie dog towns.

DIGGINGS

Diggings can be evidence of ferret presence if they are found in winter and prairie dogs have been inactive. Black-footed ferret diggings are deposits of loose soil pulled from prairie dog size burrows (about 4-inches wide) and left on the surface of the ground or snow (see photograph). A digging should be reported if:

(1) it is deposited on snow and is accompanied by "twin print" type tracks (see illustration in margins)

OR

(2) it is deposited on the ground, is more than 3 feet long, is less than 12 inches wide, and has a trough or furrow-like depression centered along its length.

REWARD CONDITIONS

The black-footed ferret is an endangered species protected by very stringent federal and state laws. The reward WILL NOT be paid for any black-footed ferret intentionally harassed, trapped, or killed by the finder. The reward will be paid to the first person who provides information leading to the discovery and verification of the first live black-footed ferret in each state. Examples of information to supply include: (1) skins and skeletons of black-footed ferrets struck accidentally by cars and found along roads, (2) photographs of ferrets or ferret diggings, or (3) observations of black-footed ferrets or ferret diggings.

The reward will not be paid to someone who was on private lands illegally.

The reward offer is limited to participating states. In the event of a tie or a question concerning the awarding of the reward, the U.S. Fish and Wildlife Service will be the final judge. The Service may elect to have the reward shared by two or more individuals if warranted. The final burden of proof, including assisting with the verification, will be the responsibility of the person making the report. The reward offer is valid from September 1, 1987 through December 31, 1990.

CONTACT To make a report or to receive more information on how to find black-footed ferrets, call or write to:

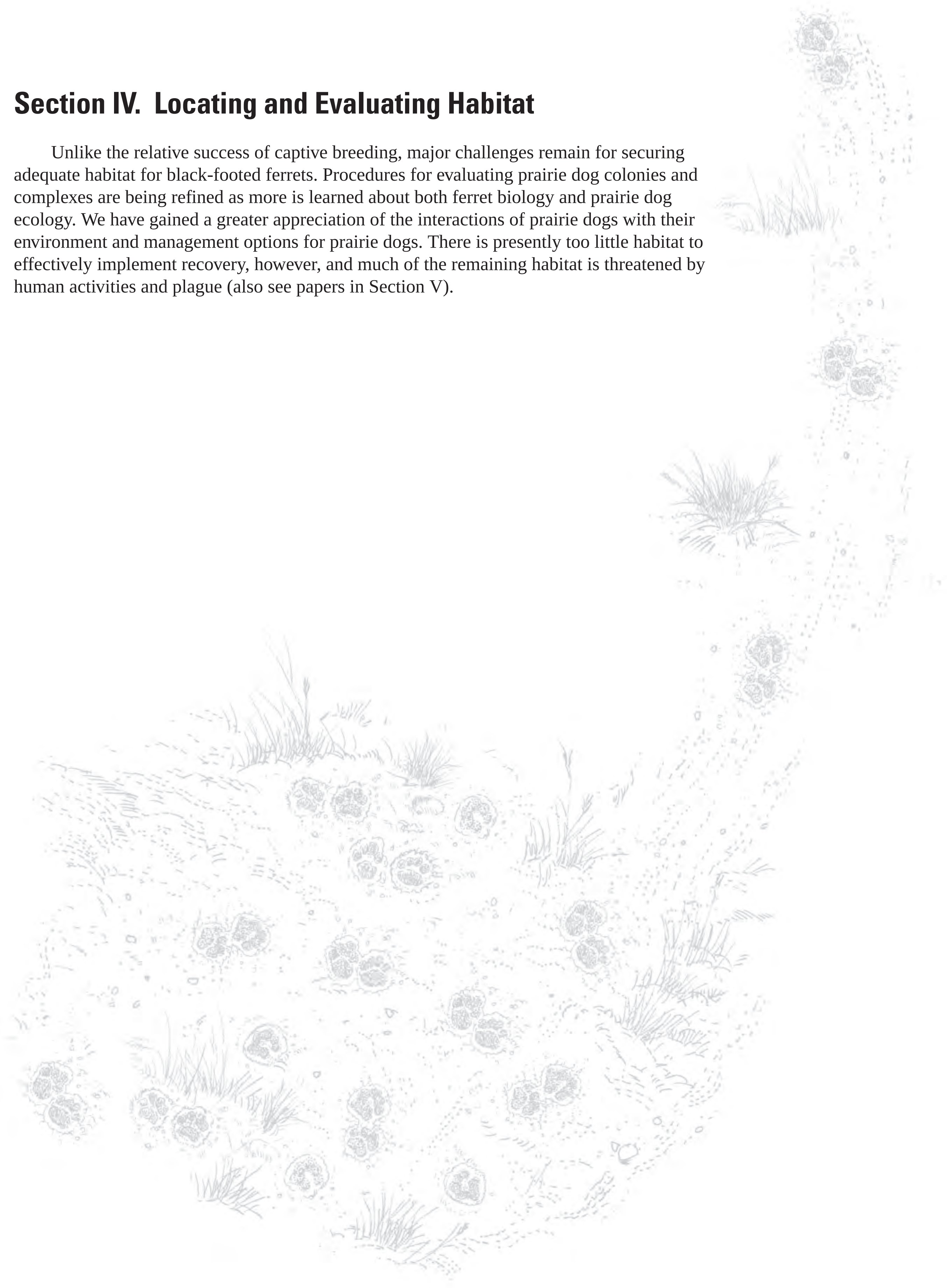
INELIGIBILITY Employees (and their relatives) of the U.S. Fish and Wildlife Service, State Conservation Agencies, and cooperators are ineligible for the reward.

Reward sponsored by the Wildlife Conservation International, a division of the New York Zoological Society.

Figure A6. The poster used to advertise the New York Zoological Society's national reward of $10,000 offered in 1989.

Section IV. Locating and Evaluating Habitat

Unlike the relative success of captive breeding, major challenges remain for securing adequate habitat for black-footed ferrets. Procedures for evaluating prairie dog colonies and complexes are being refined as more is learned about both ferret biology and prairie dog ecology. We have gained a greater appreciation of the interactions of prairie dogs with their environment and management options for prairie dogs. There is presently too little habitat to effectively implement recovery, however, and much of the remaining habitat is threatened by human activities and plague (also see papers in Section V).



Areas Where Habitat Characteristics Could Be Evaluated To Identify Potential Black-footed Ferret Reintroduction Sites and Develop Conservation Partnerships

By Robert J. Luce[1]

Abstract

This paper is an attempt to develop a new, broad list of potential black-footed ferret (*Mustela nigripes*) reintroduction sites across its historical range. I reviewed reports and publications that identified active, inactive, and potential reintroduction sites, including unpublished reports generated by State wildlife agencies and universities. I contacted local experts and reviewed the published and unpublished literature describing colony locations of three species of prairie dogs (*Cynomys* spp.). I list active reintroduction sites and others already planned and identify 70 other sites in the historical range of the black-footed ferret that might meet the biological and habitat suitability requirements for reintroduction of the species within 3–10 years, contingent upon directed management emphasis, State and Federal agency management priority, and, if on private land, landowner concurrence through agreements or incentives. I present this conceptual effort in the hope that identification of sites at this level will prompt discussion, revisions, additions, and deletions and will result in the formation of conservation partnerships that will contribute to black-footed ferret recovery.

Keywords: black-footed ferret, conservation, *Cynomys*, endangered species, *Mustela nigripes*, prairie dog, reintroduction

Introduction

Although many known, large prairie dog (*Cynomys* spp.) complexes have previously been identified, I believe that this paper is the first serious attempt to develop a new, broader list of potential reintroduction sites across the historical range of the black-footed ferret (*Mustela nigripes*). Some of these sites have been considered before, but many have not, or at least not in the same context as in the current effort. I present this conceptual effort in the hope that identification of the sites at this level will prompt discussion, revisions, additions, and deletions, and result in the formation of conservation partnerships that will contribute to black-footed ferret recovery.

Past efforts to identify sites have been constrained by the need to immediately take into account land ownership, plague history, and other factors that do not constrain the current conceptual effort. I hope that this paper prompts many who have not considered contributing to black-footed ferret recovery to get involved with a site in their locality. Several States that have not been involved in black-footed ferret recovery in the past have not previously participated in site identification.

I recognize that there are issues other than ecological ones that must be addressed when identifying potential reintroduction sites; however, I believe that recovery of the black-footed ferret depends first and foremost upon identifying and conserving areas that meet or have the potential to meet the biological parameters for establishment and long-term survival of viable populations. I believe that social and economic issues, including private land rights, economic concerns related to forage competition between livestock and prairie dogs, and others, are vitally important. I also believe, however, that a start must be made. Changes in Federal land management priorities, cooperative management planning on Federal lands, and financial incentives or regulatory assurances for private landowners or tribal governments must logically follow after habitat suitability has been established.

Recovery efforts for the endangered black-footed ferret have faced numerous and significant challenges, including extirpation of the species in the wild, development of captive breeding techniques and reintroduction methods, lack of adequate financial resources, and organizational inefficiencies (Forrest and others, 1985; Clark, 1986; U.S. Fish and Wildlife Service, 1988; Miller and others, 1996). Much work has been accomplished, and much remains to be done in these areas and others, but at present I believe that the most fundamental obstacle to meaningful recovery of the black-footed ferret in the wild is the availability of suitable habitat, both in quantity and quality; that is, prairie dog colonies of sufficient size and proximity to other colonies (Chaplin and others, 1996; Lomolino and others, 2002; Luce, 2003). There is a critical need to identify suitable sites and begin management of those sites for reintroduction and recovery. In fact, this may be the ultimate challenge to black-footed ferret recovery because it involves the greatest potential conflict with other land-use interests. Political and social barriers often surpass in difficulty those in the biological arena.

---

[1] P.O. Box 7, Sierra Vista, AZ 85636.

In the late 1980s, spurred by the need to utilize animals produced by captive breeding, biologists identified several potential reintroduction sites. In 1988–89, R. Luce (written commun., 1995) developed a list of 18 potential reintroduction sites in Wyoming by using data from a variety of sources. Conway (1989) evaluated six of those sites and concluded that only two had prairie dog numbers suitable for black-footed ferret reintroduction. Closer examination of other sites in Wyoming, as well as sites in Arizona, Colorado, South Dakota, and Utah, revealed that many were more or less unsuitable at the time of evaluation for various reasons, principally because prairie dogs did not occupy the sites to the extent that earlier evaluations had recorded or assumed (M. Lockhart, written commun., 1999–2003). Ranking of sites suitable for black-footed ferret reintroduction and recovery has emphasized the importance of large complexes of prairie dog colonies and identification of multiple sites. Additionally, it has been assumed that more densely occupied black-tailed prairie dog (*C. ludovicianus*) colonies are preferable to less dense white-tailed (*C. leucurus*) or Gunnison's (*C. gunnisoni*) prairie dog colonies and that a plague-free environment is preferable. New data documenting maintenance and/or growth of both prairie dog and black-footed ferret populations at reintroduction sites on Gunnison's and white-tailed prairie dog complexes where plague is present in Arizona (B. Van Pelt, oral commun., 2004) and Wyoming (M. Grenier, oral commun., 2004) indicate that these assumptions warrant further investigation.

A revision of the current Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) is underway, so it is important to note that I do not intend to supersede the site selection process that will be a part of the revised plan. The revised plan may include new downlisting and delisting goals for number of black-footed ferrets and number or location of reintroduction sites, but in either case a large number of potential reintroduction sites must be identified. I offer a new baseline list that includes contributions from all portions of the species' historical range, both previously overlooked sites and recently identified sites. I do not attempt to identify long-term black-footed ferret recovery needs for various areas of the species range because a rangewide delisting goal has not been identified and because a related method for apportioning recovery responsibilities among political jurisdictions has not been formalized to date (see Ernst and others, this volume).

The most promising recovery sites already have active reintroduction programs in place. I believe that several new sites with potential for adequate occupied habitat to be present within 3–10 years should be identified for each of the political jurisdictions within the historical range of the black-footed ferret. It is not appropriate to wait for a definitive answer as to the number of black-footed ferrets necessary for delisting or the amount of actual habitat that will be needed. Many more sites must be evaluated than are currently being considered because environmental unknowns, especially plague and drought, affect the viability of individual sites; therefore, longevity cannot be predicted or guaranteed. In addition, political and social attitudes may change, resulting in loss of support for maintaining adequate occupied prairie dog habitat at a given site. I identify a large number of sites so that no one site will be under pressure for rapid development, but yet the presence of the sites on the list will allow agencies to begin planning toward management of those sites, potentially allowing a significant number of them to be available for black-footed ferret reintroduction in 3–10 years.

Methods

I reviewed previous efforts that identified active, inactive, and potential black-footed ferret reintroduction sites, including the U.S. Fish and Wildlife Service (FWS) reintroduction site list (Conway, 1989; M. Lockhart, written commun., 1999–2003; fig. 1). I also reviewed published literature, including Lair and Mecham (1991), Vanderhoof and Robel (1994), Ernst (2001), and Johnson and others (2003). In addition, I reviewed available information regarding other potential sites, including unpublished reports generated by State wildlife agencies

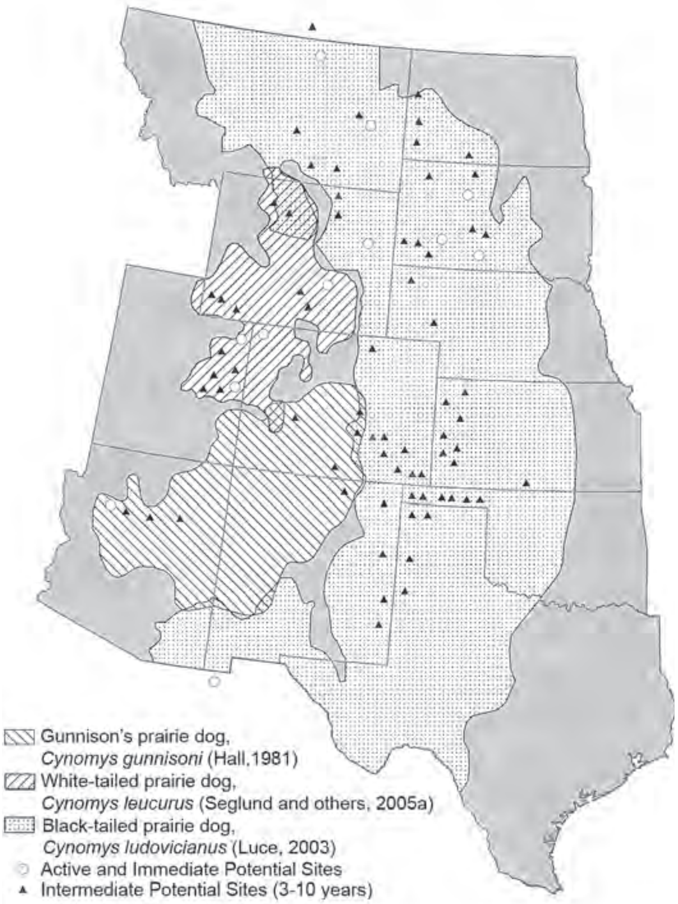


Figure 1. Location of eight active black-footed ferret (*Mustela nigripes*) reintroduction sites (1990–2004); three Immediate Potential Sites (1–3 years); and 70 Intermediate Potential Sites, at which, pending further evaluation, opportunities for reintroducing ferrets may exist in 3–10 years.

and universities, and contacted local experts. I had personal communication with Steve Whiteman, Southern Ute Tribe; Craig Knowles, FaunaWest Wildlife Consultants; Derrick Holdstock and Heather Whitlaw, Texas Parks and Wildlife Department; Julianne Hoagland, Oklahoma Department of Wildlife Conservation; Pamela Schnurr, Colorado Division of Wildlife; Dave Wagner, Northern Arizona University; Bill Woodson, U.S. Army; Mike Albee, U.S. Bureau of Land Management; Tim Byer and Dave Augustine, U.S. Forest Service; Joe Truett, Turner Endangered Species Fund; Allison Puchniak, Montana Department of Fish, Wildlife and Parks; Terry Enk, New Mexico Department of Game and Fish; Pete Gober, Randy Matchett, Scott Larson, John Nysted, and Lou Hanebury, U.S. Fish and Wildlife Service; Mark Lomolino, State University of New York, College of Environmental Science and Forestry; Amy Seglund and Craig McLaughlin, Utah Division of Wildlife Resources; Pat Fargey, Grasslands National Park, Canada; Martin Grenier, Wyoming Game and Fish Department; Tim Vosburgh, Intertribal Black-tailed Prairie Dog Coordinator; Bill Van Pelt, Arizona Game and Fish Department; Rurik List, Instituto de Ecologia, Ciudad Universitaria Coyoacan, Mexico; Travis Livieri, Prairie Wildlife Research; Mike Fritz, Nebraska Game and Parks Commission; and Sandy Hagen, North Dakota Game and Fish Department.

Information was acquired for 12 States within the historical range of the black-footed ferret, five Native American reservations, two States in Mexico, and one Canadian Province. The foundation for this effort was provided by intensive and extensive inventories and preparation of management plans for black-tailed prairie dogs, as summarized in Luce (2003); white-tailed prairie dog survey data, as summarized in Seglund and others (2005a); and Gunnison's prairie dog survey data, as summarized in Seglund and others (2005b).

I use the following terminology. Active Sites are those at which black-footed ferrets have been previously released and are being actively managed. Immediate Potential Sites are those already identified by the Black-footed Ferret Recovery Implementation Team and upon which reintroduction work has begun. Intermediate Potential Sites are those at which opportunities may exist in the 3- to 10-year time frame.

Planning efforts conducted by recovery partners require a queue of potential sites. I provide a locally specific list of all potential black-footed ferret reintroduction sites across the species' historical range but focus on Intermediate Potential Sites since these provide the next step in black-footed ferret reintroduction beyond management of Active Sites. Reintroduction efforts could begin at an Intermediate Potential Site before the minimum occupied habitat identified was available if expansion could be reasonably anticipated within a decade. Therefore, sites that are now below the minimum threshold for occupied habitat are also listed in this paper, anticipating that they have potential to meet or exceed the minimum within 10 years. Although I surmise that long-term potential sites may exist, I do not list those here.

At existing black-footed ferret reintroduction sites, as well as in State black-tailed prairie dog management plans, contiguous habitat is defined as a complex of colonies in which no colony is farther than 7 km from another colony (Biggins and others, 1993). A colony is defined as a concentration of black-tailed prairie dogs with an average density of at least 4.05 individuals/ha (Luce, 2003) or as a concentration of white-tailed prairie dogs with a minimum of 20 burrow openings/ha on 5-ha parcels (Biggins and others, 1993; Seglund and others, 2005a). Colony has not yet been defined for Gunnison's prairie dogs, but the species is biologically similar to the white-tailed prairie dog. Although this rigorous definition was not used to identify the Intermediate Potential Sites in this paper, it must be assumed that sites will be required to meet a similar standard eventually before their full potential for maintenance of a long-term, viable black-footed ferret population can be achieved.

Based on bioenergetic (Biggins and others, 1993) and behavioral considerations (R. Matchett and T. Livieri, oral commun., 2003) and known densities of the respective species, I began with the premise that the minimum adult population of 30 individuals identified in the 1988 recovery plan (U.S. Fish and Wildlife Service, 1988) might require 1,215 ha of contiguous, occupied black-tailed prairie dog habitat; 1,823 ha of contiguous, occupied Gunnison's prairie dog habitat; or 2,430 ha of contiguous, occupied white-tailed prairie dog habitat. I recognize that prairie dog densities vary between sites and at individual sites on an annual basis, but I found it necessary to use averages in this evaluation process.

I also worked from the premise that the amount of extant, occupied habitat noted above may not be necessary to identify potential reintroduction sites and perhaps begin black-footed ferret releases. I suggest that 607.5 ha of contiguous, occupied black-tailed prairie dog habitat; 911.3 ha of contiguous, occupied Gunnison's prairie dog habitat, or 1,215.0 ha of contiguous, occupied white-tailed prairie dog habitat may be sufficient to begin management planning or possible experimental release of black-footed ferrets. The choice of 50 percent was arbitrary and assumes that prairie dog colonies will grow. Of course, many other factors may affect suitability of a reintroduction site, but I believe that these rough measures may allow preliminary identification of a queue of sites that can be further evaluated.

I characterized sites in regard to the species of prairie dog present, the amount of occupied prairie dog habitat, and disease status in a manner similar to that used by M. Lockhart (written commun., 1999–2003). Many of these sites have been recently identified as a result of ongoing inventories of prairie dog habitat.

Results

Current and potential black-footed ferret reintroduction sites are listed below for U.S. States and some Native American tribal lands, Canadian Provinces, and Mexican States having historical prairie dog habitat. Each is preceded by background information related to prairie dog populations. Many sites are in the early stages of identification and mapping; some may not yet be fully mapped, and some have no data on the amount of occupied prairie dog habitat or density of prairie dogs. Sites are summarized in table 1 (Active and Immediate Potential Sites) and table 2 (Intermediate Potential Sites), and locations are illustrated in figure 1.

Arizona

Black-tailed and Gunnison's prairie dogs occurred in Arizona historically. The black-tailed prairie dog was extirpated from Arizona in the 1930s; therefore, reintroduction of black-tailed prairie dogs would be necessary before their colonies could serve as reintroduction sites for black-footed ferrets. In 2002, Wagner and Drickamer (2002) collected data from all potential sources and identified 400 locations with Gunnison's prairie dog colonies. They revisited 293 colonies in 2000 and 2001 and found that 270 were active. Gunnison's prairie dogs are located in northern Arizona from the Colorado River to Flagstaff and eastward along the Little Colorado River. No survey data are available for the Navajo Indian Reservation, which may comprise as much as one-third of the potential range.

Active Sites

Aubrey Valley

Arizona has one active black-footed ferret reintroduction site on a Gunnison's prairie dog complex in Aubrey Valley (Coconino, Yavapai, and Mojave Counties) in the northwestern part of the State (fig. 1). Reintroduction efforts began in 1996. The site is designated a black-footed ferret nonessential experimental population, and releases of captive black-footed ferrets are ongoing. Approximately 25 black-footed ferrets occur in the wild there at present. Total occupied prairie dog habitat is approximately 12,039 ha on a mixture of private, State, and Hualapai Indian Reservation lands. Monitoring at this site has not documented plague during the last 20 years, although it has been noted in the region. Prairie dog populations can be severely affected by drought at this site (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

East of Seligman

Approximately 2,502 ha of active Gunnison's prairie dog colonies were present on-site in 1992. The site is a large open grassland bisected by I-40. Occupied habitat was reduced considerably in 1996 because of a plague epizootic, but recovery began in 2001. This area is <10 km from Aubrey Valley (Wagner and Drickamer, 2002; D. Wagner, oral commun., 2003).

West of Dilkon, Navajo Indian Reservation

The Navajo Natural Heritage Program surveyed Gunnison's prairie dogs in this area to investigate its potential as a black-footed ferret reintroduction site. The survey documented approximately 3,200 ha of occupied habitat. This area was affected by plague in 1996, and there has been little recovery to date (Wagner and Drickamer, 2002; D. Wagner, oral commun., 2003).

Table 1. Sites at which black-footed ferrets (*Mustela nigripes*) have been reintroduced and are being managed (Active Sites), and sites identified by the Black-footed Ferret Recovery Implementation Team where some work preparatory to reintroduction has been done (Immediate Potential Sites).

State	Site name	Nearest town	Plague status
Active Sites			
Arizona	Aubrey Valley	Seligman	Not present
Colorado	Colorado/Utah	Dinosaur	Present
Montana	North-central Phillips County	Malta	Present
South Dakota	Cheyenne River Indian Reservation		
	Conata Basin/Badlands National Park	Wall	Not present
	Rosebud Indian Reservation	Winner	Not present
Utah	Colorado/Utah	Dinosaur, Colo.	Present
Wyoming	Shirley Basin	Medicine Bow	Present
Chihuahua, Mexico	Janos	Janos	Not present
Immediate Potential Sites			
Montana	Custer Creek	Miles City	Unknown
Utah	Cisco Desert	Green River	Present
Wyoming	Thunder Basin National Grassland	Bill	Present

Table 2. Sites at which, pending further evaluation, opportunities for reintroducing black-footed ferrets (*Mustela nigripes*) may exist in 3–10 years (Intermediate Potential Sites; *n* = 70).

State or Province	Site name	Nearest town	Plague status
Arizona	East of Seligman	Seligman	Present
	West of Dilkon, Navajo Indian Reservation	Dilkon	Present
	West of Wupatki National Monument	Flagstaff	Present
Colorado	Pueblo County	Pueblo	Present
	Weld County	Greeley	Present
	Bent County	Lamar	Present
	Baca County	Springfield	Present
	Crowley County	Rocky Ford	Present
	Pueblo Army Depot	Pueblo	Present
	Fort Carson	Colorado Springs	Present
	Comanche National Grassland, Carrizo Unit	Pritchett	Present
	Comanche National Grassland, Timpas Unit, and Pinon Canyon Maneuver Site	La Junta	Present
	Cimarron National Grassland	Springfield	Present
	BLM Twin Lakes Allotment	Alamosa	Present
	Parlin	Gunnison	Present
Kansas	Z-Bar Ranch	Medicine Lodge	Plague free
	Logan County	Colby	Plague free
	Northern Kearny County	Garden City	Plague free
	Greeley County	Horace	Plague free
	Rawlins County	Atwood	Plague free
	Hamilton County	Syracuse	Plague free
	Southern Kearny County	Garden City	Plague free
	Sherman County	Colby	Plague free
Montana	Leachman complex	Billings	Present
	Northern Cheyenne Indian Reservation	Colstrip	Present
	Miles City BLM District	Miles City	Present
	Fort Benton-Roundup-Harlowton area	Roundup	Present
Nebraska	Blue Creek Ranch	Oshkosh	Plague free
	Oglala National Grassland	Chadron	Plague free
New Mexico	Vermejo Park Ranch	Raton	Unknown
	Quay/Curry County interface	Tucumcari	Unknown
	Roosevelt County/Grulla National Wildlife Refuge	Portales	Unknown
	Lea County	Lovington	Unknown
	Union County	Clayton	Unknown
North Dakota	Horse Creek area, Little Missouri National Grassland	Williston	Unknown
	Standing Rock Indian Reservation	North Lemmon	Unknown
	South Unit, Theodore Roosevelt National Park	Dickinson	Plague free
	Little Missouri River	Bowman	Plague free

Table 2. Sites at which, pending further evaluation, opportunities for reintroducing black-footed ferrets (*Mustela nigripes*) may exist in 3–10 years (Intermediate Potential Sites; *n* = 70)—Concluded.

State or province	Site name	Nearest town	Plague status
Oklahoma	Southwest Cimarron County	Boise City	Plague free
	Texas County No. 1	Guymon	Plague free
	Texas County No. 2	Guymon	Plague free
	Beaver County No. 1	Beaver	Plague free
	Beaver County No. 2	Beaver	Plague free
South Dakota	Pine Ridge Indian Reservation	Pine Ridge	Plague free
	Standing Rock Indian Reservation	Lemmon	Plague free
	Lower Brule Indian Reservation	Pierre	Plague free
	Wind Cave National Park	Hot Springs	Plague free
	Grand River National Grassland	Lodgepole	Plague free
	Bad River Ranches	Pierre	Plague free
	Smithwick area, Buffalo Gap National Grassland	Hot Springs	Plague free
Texas	Rita Blanca National Grassland	Dalhart	Unknown
	Muleshoe National Wildlife Refuge	Lubbock	Present
	Sherman County	Dumas	Unknown
	Deaf Smith County	Amarillo	Unknown
Utah	Buckhorn and Crescent Junction	Price	Present
	Twelvemile Flat	Green River	Present
	Eightmile Flat (Myton Bench)	Green River	Present
	Sunshine Bench/Brush Creek	Green River	Present
	Buckhorn Flat	Price	Present
Wyoming	Meeteetse	Meeteetse	Present
	Bolton Ranch	Saratoga	Present
	Carter	Kemmerer	Present
	Cumberland	Kemmerer	Present
	Fifteenmile	Worland	Present
	Flaming Gorge	Green River	Present
	Shamrock Hills	Rawlins	Present
	Kaycee	Kaycee	Unknown
	Sheridan Local Training Center	Sheridan	Unknown
Saskatchewan, Canada	Grasslands National Park	Swift Current	Unknown

West of Wupatki National Monument

Gunnison's prairie dogs are present at this site north of Flagstaff. A complex of 950 ha was mapped in 2001. Plague has occurred, but the extent has not been quantified (Wagner and Drickamer, 2002; D. Wagner, oral commun., 2003).

Colorado

Black-tailed prairie dogs, white-tailed prairie dogs, and Gunnison's prairie dogs occur in Colorado. Complete location data are not available for Gunnison's prairie dogs since some potential habitat in southwestern Colorado has not been surveyed. White-tailed prairie dogs are also currently being surveyed in northwestern Colorado. Black-tailed prairie dogs occur in all counties in the historical range in the eastern one-third of the State, and recent surveys indicate 255,596 ha of occupied habitat (Colorado Division of Wildlife, 2003). Location data from that survey are not available to the author at this time, however. EDAW, Inc. (2000) identified the 10 counties with the largest amount of active, occupied habitat in the State: Pueblo (8,989 ha), Weld (8,146 ha), Bent (6,914 ha), Baca (5,816 ha), Crowley (5,475 ha), Adams (5,372 ha), Prowers (5,161 ha), Boulder (4,668 ha), Cheyenne (3,717 ha), and Kiowa (3,629 ha). EDAW, Inc. (2000) identified 17 colonies >405 ha and 45 colonies from 203 to 405 ha in the black-tailed prairie dog range in Colorado.

Active Sites

Colorado/Utah

White-tailed prairie dogs occupy the only active black-footed ferret reintroduction site in Colorado. The site is located in northwestern Colorado in Moffat and Rio Blanco Counties and extends into Utah (Uintah County) and Wyoming (Sweetwater County). The Wyoming portion of the site, called Kinney Rim, has virtually no active colonies at the current time. Reintroduction efforts began in 1998. The site is designated a black-footed ferret nonessential, experimental population, and releases of captive black-footed ferrets are ongoing. A small population of black-footed ferrets occurs in the wild there at present. Total occupied prairie dog habitat is approximately 20,250 ha, primarily on U.S. Bureau of Land Management (BLM) land, and plague is present. Potential habitat present in the Colorado portion of this site is estimated at 45,553 ha (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

Pueblo County

Black-tailed prairie dogs occupy this site. The northern half of the county, north of the City of Pueblo, has the largest concentration of colonies and the majority of the 8,989 ha of colonies identified in the county (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Weld County

Black-tailed prairie dogs occupy this site. The northeastern half of the county, northeast of the City of Greeley, has the largest concentration of colonies and the majority of the 8,146 ha of colonies identified in the county (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Bent County

Large black-tailed prairie dog colonies occur in the northern and western parts of the county, encompassing the majority of the 6,914 ha identified (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Baca County

The western one-half of the county, centered on the town of Pritchett, has the largest concentration of black-tailed prairie dog colonies and has the majority of the 5,816 ha identified in the county (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Crowley County

Large black-tailed prairie dog colonies occur in several places in the county, encompassing 5,475 ha (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Pueblo Army Depot

Black-tailed prairie dogs occupy this site, which is on a U.S. Army installation. Approximately 1,066 ha of occupied habitat were present before a plague outbreak in 2003. The site is managed by the military and is protected from shooting and poisoning except where black-tailed prairie dogs may constitute a human health hazard (B. Woodson, oral commun., 2003). A large area of occupied habitat also occurs on private lands adjacent to Pueblo Army Depot in El Paso County (EDAW, Inc., 2000).

Fort Carson

Black-tailed prairie dogs occupy this site, which is on a U.S. Army installation. Approximately 1,418 ha of occupied habitat were present before a plague outbreak occurred in 2002 or 2003. The site is managed by the military and is protected from shooting and poisoning except where black-tailed prairie dogs may constitute a human health hazard (B. Woodson, oral commun., 2003). A large area of occupied habitat also occurs on private lands adjacent to Fort Carson, particularly along the southern boundary in Pueblo County (EDAW, Inc., 2000).

Comanche National Grassland, Carrizo Unit

Recent GIS analyses identified 46,395 ha of potential black-tailed prairie dog habitat on this site in Baca County. Potential habitat was defined as land with clay or loamy soil and <5 percent slope. Of this potential habitat, 1,622 ha are currently occupied, with an additional 450 ha occupied outside of potential habitat (primarily on lands mapped as sandy soils, most likely because of inaccurate generalities in the soil map). The Carrizo Unit has extremely fragmented land ownership. Intermingled private lands have even higher densities of colonies (due to higher grazing intensity), but landowners have strongly negative attitudes toward black-tailed prairie dogs. Approximately 2,076 ha of occupied black-tailed prairie dog habitat occurs on National Forest lands, and the amount of occupied habitat on intermingled private lands is unknown (D. Augustine, written commun., 2003).

Comanche National Grassland, Timpas Unit, and Pinon Canyon Maneuver Site

Black-tailed prairie dogs occupy this site, which is on the Timpas Unit and the adjoining U.S. Army Pinon Canyon Maneuver Site. Together these areas provide a large block of land in public ownership with little fragmentation. The Timpas Unit includes a number of private inholdings but is far less fragmented than the Carrizo Unit (above). The amount of occupied habitat in the Timpas Unit is lower than in the past because of plague. A total of 35,917 ha of potential habitat exists, of which 192 ha are currently occupied. An additional 41 ha are outside the area mapped as suitable habitat, for a total of 233 ha on the Timpas Unit. Occupied habitat on the Pinon Canyon Maneuver Site totaled 143 ha when last mapped (D. Augustine, written commun., 2003).

Cimarron National Grassland

Black-tailed prairie dogs occupy this site, which has approximately 16,200 ha of potential habitat, 1,296 ha of which were occupied in 2003. The area is bounded on the north by cropland and on the south by riparian/sand sagebrush (*Artemisia filifolia*) habitat. The Cimarron is separated from the Comanche by sand sagebrush habitat unsuitable for black-tailed prairie dog expansion (D. Augustine, written commun., 2003).

Bureau of Land Management Twin Lakes Allotment

Gunnison's prairie dogs occur at this site on public land in Conejos County, approximately 32 km south of Alamosa. The area supports a large complex of colonies dating back to the 1970s, many of which are old or inactive. Existing occupied habitat is approximately 512 ha (M. Albee, oral commun., 2003).

Parlin

Gunnison's prairie dogs occur at this site, which is on public land 19 km southeast of Gunnison in Gunnison County. The amount of occupied habitat in 1980 was 497 ha (M. Albee, oral commun., 2003).

Kansas

Only black-tailed prairie dogs occur in Kansas. Recent surveys estimate 52,861 ha of occupied habitat in western Kansas (Kansas Black-tailed Prairie Dog Working Group, 2002). The estimate of suitable habitat in Kansas based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 60,181 ha.

Intermediate Sites

Z-Bar Ranch

Black-tailed prairie dogs occupy this site, which is on property owned by Turner Enterprises, Inc., approximately 40 km southwest of Medicine Lodge in Barber County. The site currently supports 101 ha of occupied habitat and is growing steadily. Grassland conservation and black-tailed prairie dog expansion are high priority management objectives (J. Truett, oral commun., 2003).

Logan County

This county contained the largest complex (3,522 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Northern Kearny County

The northern part of this county contained the second largest complex (1,104 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Greeley County

This county contained the third largest complex (826 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Rawlins County

This county contained the fourth largest complex (448 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Hamilton County

This county contained the fifth largest complex (423 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Southern Kearny County

The southern part of this county contained the sixth largest complex (400 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Sherman County

This county had the highest number of colonies and highest occupied area in the 1990–92 survey: 60 colonies and 1,420 ha (Vanderhoof and Robel, 1992, 1994). It also had significant occupied black-tailed prairie dog habitat in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Montana

Both black-tailed and white-tailed prairie dogs occur in Montana. White-tailed prairie dogs are confined to a very small area near the border with Wyoming and occupy roughly 40 ha of habitat at the present time; therefore, no black-footed ferret reintroduction potential exists for the foreseeable future. Black-tailed prairie dogs occur in the eastern part of the State, and the best estimate of occupied area is 36,450 ha (Montana Prairie Dog Working Group, 2002). The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 97,349 ha.

Active Sites

North-central Phillips County

Black-tailed prairie dogs occupy this site. Black-footed ferret releases have occurred since 1994. Occupied prairie dog habitat was 12,014 ha in the mid-1990s, with 5,457 ha occurring on Fort Belknap Indian Reservation, 4,472 ha on BLM lands, and 2,085 ha on Charles M. Russell National Wildlife Refuge. The area was heavily affected by plague in the late 1990s. The black-footed ferret population is very low at the current time. Land ownership is mixed private, Federal, and tribal (M. Lockhart, written commun., 1999–2003).

Immediate Potential Sites

Custer Creek

Black-tailed prairie dogs occupy this site in Prairie and Custer Counties, which contains >100 colonies and 1,705 ha of occupied habitat on a mixture of State, private, and BLM lands. Plague has not been documented since 1996. Since this site is in an area of checkerboard land status, private interests control the site potential (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

The following locations were identified in the Conservation Plan for Black-tailed and White-tailed Prairie Dogs in Montana (Montana Prairie Dog Working Group, 2002) as 4 of the 10 largest known prairie dog complexes in Montana in 2000.

Leachman Complex

This site is entirely on tribal land in the northwest portion of the Crow Indian Reservation in Yellowstone and Big Horn Counties, and once supported an estimated 4,050–4,860 ha of occupied prairie dog habitat (L. Hanebury, oral commun., 2003). The site included >2,835 ha of occupied prairie dog habitat in recent times but suffered a plague outbreak prior to 2003. Approximately 2,430 ha remained in two colonies in the southwest and central portions of the area in 2003. With translocations, this complex could be viable within a few years (L. Hanebury, oral commun., 2003). Since surveys of suitable habitat on the Crow Indian Reservation have not been completed, sites other than the Leachman site may also exist (L. Hanebury, oral commun., 2003).

Northern Cheyenne Indian Reservation

Suitable habitat exists on the Reservation along the upper Tongue River in Big Horn and Rosebud Counties as well as on adjacent U.S. Forest Service and private lands. Occupied habitat exceeded 5,265 ha prior to a recent plague outbreak. With the help of translocations, this site grew to approximately 2,025 ha in 2003 (L. Hanebury, oral commun., 2003).

Miles City Bureau of Land Management District

Potential habitat exists in Custer and Prairie Counties. This site is mixed private and BLM lands and supported approximately 2,430 ha of prairie dogs in 2000; however, recent plague outbreaks have reduced the size of this complex to approximately 1,337 ha. A change in land ownership resulted in reduced access for mapping, which may have exaggerated the apparent decline in occupied habitat (L. Hanebury, oral commun., 2003).

Fort Benton-Roundup-Harlowton Area

Suitable habitat exists along the upper Musselshell River in Yellowstone, Stillwater, Musselshell, Golden Valley, Wheatland, and Petroleum Counties. The area is mixed private, BLM, and FWS lands and supported >2,430 ha of prairie dogs in 2000 (L. Hanebury, oral commun., 2003).

Nebraska

Only black-tailed prairie dogs occur in Nebraska. Recent surveys estimate 32,400 ha of occupied habitat (M. Fritz, oral commun., 2003) in western Nebraska. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 55,588 ha.

Intermediate Potential Sites

Blue Creek Ranch

This site, which is owned by Turner Enterprises, Inc., is 16 km northeast of Oshkosh and currently has 8 ha of occupied habitat, which is expanding. Grassland conservation and black-tailed prairie dog expansion are high management priorities (J. Truett, oral commun., 2003).

Oglala National Grassland

This site is located in Sioux and Dawes Counties and currently has 284 ha of occupied black-tailed prairie dog habitat. The Oglala National Grassland will require time to expand existing prairie dog habitat and to consolidate the land base to improve the management potential (S. Larson, written commun., 2003).

New Mexico

Black-tailed and Gunnison's prairie dogs occur in New Mexico. Recent black-tailed prairie dog surveys estimate 24,300 ha of occupied habitat (Johnson and others, 2003) in eastern New Mexico. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 35,288 ha. Surveys are ongoing for Gunnison's prairie dog, but there is no estimate of current occupied habitat.

Intermediate Potential Sites

Vermejo Park Ranch

This site, which is owned by Turner Enterprises, Inc., is located 40 km southwest of Raton and currently has 689 ha of occupied habitat, which is expanding rapidly. Grassland conservation and black-tailed prairie dog expansion are high priorities (J. Truett, oral commun., 2003).

Quay/Curry County Interface

This site is south of Tucumcari and contains >3,848 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 19 ha, and the maximum area of a single colony is 152 ha (Johnson and others, 2003).

Roosevelt County/Grulla National Wildlife Refuge

This site is south of Portales and contains >5,265 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 35 ha, and the maximum size of a single colony is 339 ha (Johnson and others, 2003).

Lea County

This site is northeast of Lovington and contains approximately 9,720 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 60 ha, and the maximum area of a single colony is 956 ha (Johnson and others, 2003). Plague has recently been active in this area, but impacts have not been quantified (P. Gober, oral commun., 2003).

Union County

This site is southwest of Clayton and contains approximately 3,240 ha of occupied habitat. The mean size of colonies is 41 ha, and the maximum area of a single colony is 292 ha (Johnson and others, 2003).

North Dakota

Only black-tailed prairie dogs occur in North Dakota. Recent surveys estimate 8,303 ha of occupied habitat (Knowles, 2003) in western North Dakota. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 40,723 ha.

Intermediate Potential Sites

Horse Creek Area, Little Missouri National Grassland

Black-tailed prairie dogs occupy 162 ha at this site in McKenzie County in western North Dakota. The site has strong potential to reach biological readiness for black-footed ferret reintroduction within 10 years, but local support cannot be predicted at this time. The site is included in the most recent land management plans for Little Missouri National Grassland and is plague free (S. Larson, written commun., 2003).

Standing Rock Indian Reservation

Black-tailed prairie dogs occupy 1,215 ha at this site in Sioux County. Colonies are scattered over a large area, and the land base is a checkerboard of private and tribal lands. The area is plague free (S. Larson, written commun., 2003).

South Unit, Theodore Roosevelt National Park

Black-tailed prairie dogs occupy 729 ha at this site in Billings County. In 2002, 61 active colonies were mapped (Knowles, 2003). Knowles (2003) predicted that the site potential on the national park is >2,633 occupied ha based on the amount of suitable habitat present. Additional suitable habitat occurs on adjacent private land, and the area is plague free (Knowles, 2003).

Little Missouri River

Black-tailed prairie dogs occupy this site in Slope County. The site had 345 ha of occupied habitat in 2002. Significant biological potential exists if private land issues can be addressed. The area is plague free (Knowles, 2003).

Oklahoma

Only black-tailed prairie dogs occur in Oklahoma. Recent surveys estimate 26,007 ha of occupied habitat (J. Hoagland, oral commun., 2003) in western Oklahoma. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 27,806 ha.

Intermediate Potential Sites

Sites in Oklahoma have previously been described as clusters of colonies (M. Lomolino, written commun., 2003).

Cimarron County

This site is in the southwestern corner of the county. Cluster A had 12 colonies totaling 345 ha, and Cluster B had 6 colonies with a total of 652 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Texas County No. 1

This site is in the north-central part of the county. Cluster C had 12 colonies with a total of 332 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Texas County No. 2

This site is in the east-central part of the county. Cluster D had 18 colonies with a total of 302 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Beaver County No. 1

This site is in the east-central part of the county. Cluster E had 10 colonies with a total of 93 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Beaver County No. 2

This site is in the south-central part of the county. Cluster F had 34 colonies with a total of 319 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

South Dakota

Only black-tailed prairie dogs occur in South Dakota. A 2001 survey estimated 64,800 ha of occupied habitat (South Dakota Prairie Dog Work Group, 2001) in western South Dakota. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 80,786 ha.

Active Sites

Cheyenne River Indian Reservation

Black-tailed prairie dogs occupy this site in Dewey and Ziebach Counties. Total occupied habitat is 17,861 ha in three separate complexes, one of which is 8,424 ha. An operational prairie management program is currently pursuing black-footed ferret reintroduction. There is no history of plague in the area (M. Lockhart, written commun., 1999–2003).

Conata Basin/Badlands National Park

Black-tailed prairie dogs occupy this site in Pennington, Shannon, and Jackson Counties. Total occupied habitat is 6,116 ha, with 4,779 ha on U.S. Forest Service lands and 1,337 ha on National Park Service lands. The estimated potential for the area based on suitable habitat is 7,128 ha. There is no history of plague in the area (M. Lockhart, written commun., 1999–2003).

Rosebud Indian Reservation

Black-tailed prairie dogs occupy 28,350 ha at this site in Todd and Mellette Counties, 18,225 ha of which is on tribal trust lands. There is no history of plague in the area (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

Pine Ridge Indian Reservation

Black-tailed prairie dogs occupy 20,250–40,500 ha on tribal lands at this site in Shannon County. The site has the biological capacity to support a large black-footed ferret population but may be constrained by social, cultural, and political factors (S. Larson, written commun., 2003).

Standing Rock Indian Reservation

Black-tailed prairie dogs occupy 2,835 ha at this site in Corson County. Black-tailed prairie dogs are scattered over a large area, and the land base is a mixture of private and tribal. There is no history of plague in the area (S. Larson, written commun., 2003).

Lower Brule Indian Reservation

Black-tailed prairie dogs occupy 11,745 ha at this site in Stanley and Lyman Counties. There is no history of plague in the area (S. Larson, written commun., 2003).

Wind Cave National Park

Black-tailed prairie dogs occupy 689 ha at this site in Custer County. Biologically, this site could be ready for black-footed ferret reintroduction within a few years, and the National Park Service is supportive. There is no history of plague in the area (S. Larson, written commun., 2003).

Grand River National Grassland

Black-tailed prairie dogs occupy 648 ha at this site in Perkins and Corson Counties. Biologically, this site is not ready for black-footed ferret reintroduction, as it needs time for black-tailed prairie dogs to expand occupied habitat. The U.S. Forest Service needs to consolidate its land base; however, it has identified the site for prairie dog expansion in the most recent land management plan. There is no history of plague in the area (S. Larson, written commun., 2003).

Bad River Ranches

Black-tailed prairie dogs occupy this site on lands owned by Turner Enterprises, Inc., in Stanley and Jones Counties, 16 km southwest of Pierre. The site currently has 506 ha of occupied habitat and is growing steadily. Grassland conservation and black-tailed prairie dog expansion are high priorities. There is no history of plague in the area (J. Truett, oral commun., 2003).

Smithwick Area, Buffalo Gap National Grassland, Fall River Ranger District

Black-tailed prairie dogs occupy 405 ha at this site in Custer County. From a biological standpoint, the site could be ready for black-footed ferret reintroduction within 5 years. The site was included in the most recent land management plan for Buffalo Gap National Grassland. There is no history of plague in the area (S. Larson, written commun., 2003).

Texas

Only black-tailed prairie dogs occur in Texas. Ongoing surveys currently estimate 79,785 ha of occupied habitat in western Texas (D. Holdstock, oral commun., 2003). The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 118,717 ha.

Intermediate Potential Sites

Rita Blanca National Grassland

Black-tailed prairie dogs occupy this site north of Dalhart in Dallam County. The site was identified by Lair and Mecham (1991) as having >4,050 ha of occupied habitat, with 49 colonies >41 ha in size and >1.0 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Muleshoe National Wildlife Refuge

Black-tailed prairie dogs occupy this site northwest of Lubbock in Bailey County. It was identified by Lair and Mecham (1991) as having >2,835 ha of occupied habitat, with 25 colonies >41 ha in size and >1.0 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Sherman County

Black-tailed prairie dogs occupy this site north of Dumas. It was identified by Lair and Mecham (1991) as having >3,240 ha of occupied habitat, with 32 colonies >41 ha in size and 1.5 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Deaf Smith County

Black-tailed prairie dogs occupy this site southwest of Amarillo. It was identified in Lair and Mecham (1991) as having >5,670 ha of occupied habitat, with 55 colonies >41 ha in size and 1.5 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Utah

Gunnison's prairie dogs and white-tailed prairie dogs occur in Utah. Data on locations and occupied area are still being developed for both species.

Active Sites

There is one active black-footed ferret reintroduction site in Utah (see discussion under Colorado).

Immediate Potential Sites

Cisco Desert

White-tailed prairie dogs occur at this potential site identified by the Black-footed Ferret Recovery Program. The site was mapped in 1986 (Boschen, 1986) and again in 2002 (Seglund and others, 2005a). The site is on public land in Grand County in east-central Utah along I-70 from east of Green River to the Colorado border. Land ownership is mixed private, State, and Federal (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

Buckhorn and Crescent Junction

White-tailed prairie dogs occupy this site in Emery and Grand Counties in south-central Utah. According to C. McLaughlin (oral commun., 2003), Cedar Creek Associates mapped 7,644 ha, including both active and inactive colonies, in this complex on public lands in 1985. The area mapped extended south of Huntington to I-70 along State Highway 10, east to State Highway 6, and along I-70 to Thompson Springs. In 2002, mapping within the same area recorded 7,881 ha, including active and inactive colonies, approximately a 3 percent increase from 1985 (C. McLaughlin, written commun., 2003).

Twelvemile Flat

White-tailed prairie dogs occur at this site on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. Twelvemile Flat contained 363 ha of occupied habitat in 1985. The site was resurveyed in 1992–93 (Cranney and Day, 1994) and found to have 771 ha of occupied habitat, slightly over double the amount present in 1985. In 2002, mapping located 365 ha of occupied habitat (C. McLaughlin, written commun., 2003).

Eightmile Flat (Myton Bench)

White-tailed prairie dogs occur at this site on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. Eightmile Flat contained 2,673 ha of occupied habitat in 1985. The site was resurveyed in 1999 and found to have increased by 9 percent, to 2,936 ha of occupied habitat (C. McLaughlin, written commun., 2003).

Sunshine Bench/Brush Creek

White-tailed prairie dogs occur at these sites on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. The sites were mapped to evaluate their suitability for black-footed ferret reintroduction in 1992–93 (Cranney and Day, 1994). The Sunshine Bench complex contained 2,085 ha of occupied habitat in 1992–93, while the adjacent Brush Creek area contained 145 ha of occupied habitat. The combined occupied area of Sunshine Bench and Brush Creek was 7,837 ha in 2002 (C. McLaughlin, written commun., 2003).

Buckhorn Flat

White-tailed prairie dogs occur at this site on public lands 56 km south of Price. The estimated occupied habitat at the site is 2,412 ha (A. Seglund, written commun., 2003).

Wyoming

Black-tailed and white-tailed prairie dogs occur in Wyoming. Black-tailed prairie dogs occur in the eastern one-third of the State. Recent occupied habitat estimates range widely, but the current estimate is 50,625 ha (M. Grenier, written commun., 2003). The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 64,059 ha. White-tailed prairie dogs occur in the west-central part of the State, and surveys are underway to estimate occupied habitat.

Active Sites

Shirley Basin

Shirley Basin/Medicine Bow is the only active black-footed ferret reintroduction site in Wyoming and occurs in the white-tailed prairie dog range. The site was fully mapped in 1989 (Conway, 1989) and again in 1990 by using a combination of aerial transects and ground verification (Hnilicka and Luce, 1992). In 1990, intensive mapping showed the complex to contain 59,726 ha (Parrish and Luce, 1990). Captive-bred black-footed ferrets were released from 1991 to 1994, and the highest number of black-footed ferrets found on subsequent surveys was in 2004, when 85 individuals were located during spotlight surveys (Grenier and others, 2004) of less than 20 percent of the occupied habitat (based on 1990 mapping data). Therefore, considerable potential exists for a large, contiguous population of black-footed ferrets or several subpopulations. It is important to note that both prairie dogs and black-footed ferrets have persisted with plague present since at least 1987 (Orabona-Cerovski, 1991).

Immediate Potential Sites

Thunder Basin National Grassland

Black-tailed prairie dogs occur at this site in Campbell, Converse, and Weston Counties. The site is identified as a black-footed ferret reintroduction site in the current Forest Plan for the Medicine Bow National Forest/Thunder Basin National Grassland. There was no history of plague before 2001 when an extensive die-off occurred, reducing occupied habitat by over 4,050 ha. Recovery is occurring. Prior to the plague outbreak, occupied black-tailed prairie dog habitat was 8,079 ha, including 7,290 ha on U.S. Forest Service land and 789 ha on State land. The U.S. Forest Service estimates that there are 193,590 ha of potential habitat on its lands in this area of Wyoming (T. Byer, written commun., 2003).

Intermediate Potential Sites

Meeteetse

White-tailed prairie dogs occupy this site west of Meeteetse in Park County. This site, from which all of the black-footed ferret captive breeding stock was taken, had 4,930 ha of occupied habitat in 1982, just after black-footed ferrets were first discovered, and a high population of 129 black-footed ferrets (43 adults, 25 litters) in 1984. Because of plague in white-tailed prairie dogs, occupied habitat was reduced to roughly 2,029 ha by 1989, 2 years after all extant black-footed ferrets were captured for captive breeding (Black-footed Ferret Advisory Team, 1990). The site has not shown significant recovery of prairie dogs since 1989 (Biggins, 2003). The habitat capability of the site remains, including old burrow systems, so the potential exists for recovery to sufficient occupied habitat for black-footed ferret reintroduction within 10 years.

Bolton Ranch

White-tailed prairie dogs occupy this site west of Saratoga in Carbon County. Land ownership is a checkerboard of public and private lands. The site had 4,500 ha of occupied habitat in 1989 when it was first surveyed (Conway, 1989). No surveys have been conducted since then (Grenier and others, 2003; R. Luce, written commun., 1995).

Carter

White-tailed prairie dogs occupy this site 32 km southeast of Kemmerer, on BLM lands in Lincoln County. The site has not been fully mapped or surveyed to determine prairie dog density. It contained more than 4,050 ha of occupied habitat when partially mapped in the 1980s (Grenier and others, 2003; R. Luce, written commun., 1995). The Carter site is potentially connected to another site (Moxa) which is 32 km north of Kemmerer, indicating that an extremely large complex may exist in this area. Moxa was identified in the mid-1990s when 17,415 ha of occupied habitat were mapped, and the site has not been resurveyed (Grenier and others, 2003; B. Luce, unpub. data, 1995).

Cumberland

White-tailed prairie dogs occupy this site southwest of Kemmerer in Lincoln County. Land ownership is a checkerboard of public and private lands. The site was fully mapped and preliminary density data were collected in the 1980s (Clark and Campbell, 1981). Occupied habitat was 4,293 ha. The site has not been remapped.

Fifteenmile

White-tailed prairie dogs occupy this site on BLM land 40 km west of Worland in Hot Springs County. The site contained 3,078 ha of occupied habitat when mapped in the 1980s and has not been remapped (Grenier and others, 2003; R. Luce, written commun., 1995).

Flaming Gorge

White-tailed prairie dogs occupy this site on BLM land 64 km south of Green River in Sweetwater County. The site was intensively mapped in 1989 and contained 3,049 ha of occupied habitat (Martin and Luce, 1990). It has not been remapped.

Shamrock Hills

White-tailed prairie dogs occupy this site on BLM land 16 km north of Rawlins in Carbon County. The site was mapped in the 1980s and had >4,050 ha of occupied habitat. The site has not been remapped (Grenier and others, 2003; R. Luce, written commun., 1995).

Kaycee

Black-tailed prairie dogs occupy this site west of the town of Kaycee in Johnson County, primarily on private land. This site was discovered recently and has not been mapped, but it is estimated that >1,215 ha of occupied habitat are present (R. Luce, unpub. data, 2003).

Sheridan Local Training Center

Black-tailed prairie dogs occupy this site on a U.S. Army installation adjacent to Sheridan in Sheridan County. The site contained 284 ha of occupied habitat in 2001, and adjacent private and State lands had a substantial amount of additional occupied habitat (R. Luce, unpub. data, 2003).

Canada

Only black-tailed prairie dogs occur in Canada, which is the northern extent of the range of the species.

Intermediate Potential Sites

Grasslands National Park and Vicinity

Black-tailed prairie dogs occur at this site in Saskatchewan, 160 km south of Swift Current. The site has 25 colonies containing a minimum of 1,044 ha. It has been partially mapped since 1993 but was fully mapped for comparative purposes from 1998 to 2002 and had a stable occupied area for that time period (P. Fargey, written commun., 2003).

Mexico

Black-tailed prairie dogs occur in northern Mexico, the southern extent of the range, and are the only species of prairie dog in Mexico in the historical range of the black-footed ferret.

Active Sites

Janos

Black-tailed prairie dogs occur at this site north of Nuevo Casas Grandes in Chihuahua. Estimated occupied prairie dog habitat is 19,845 ha, and the potential suitable habitat is 55,080 ha. Land ownership is divided between Federal Ejidos and private ownership. This is a large prairie dog complex and may have the potential for one contiguous black-footed ferret population or several subpopulations. No management plan exists for the area (R. List, oral commun., 2003).

Intermediate Potential Sites

There are no Intermediate Potential Sites in Mexico.

Discussion

It is clear from past efforts that a “best and only” methodology for successful black-footed ferret reintroduction has not been unequivocally established. The 1988 recovery plan (U.S. Fish and Wildlife Service, 1988) encourages experimentation. It also emphasizes a management philosophy important for both establishing and maintaining reintroduced populations whereby the broadest possible distribution of black-footed ferrets might be achieved. This risk management approach is important to protect the species overall from adverse impacts that may occur locally, especially disease.

Preparation of this paper does not constitute a proposed State or Federal action at any of the proposed sites; it is merely a conceptual approach to aid in black-footed ferret recovery. Many steps will be required before any site can eventually receive ferrets; however, I do not believe that it is necessary or appropriate to wait for final biological, social, and political issues to be addressed at a given site in order for it to be considered for the list of potential reintroduction sites. This conceptual exercise identifies sites based entirely on either a minimum area of occupied prairie dog habitat or a small but increasing prairie dog population at a site that has the habitat characteristics necessary to support black-footed ferrets. I recognize that myriad actions would be necessary before black-footed ferrets could actually be released at a given site, especially where private lands are involved.

The general limitation of lack of habitat or habitat availability is shared with many other species. But in the case of the black-footed ferret, which is a highly specialized prey/habitat obligate of prairie dogs, dependence has proven to be especially catastrophic because of the dramatic reduction of its prey over the past century by adverse land-use practices such as prairie conversion to cropland, poisoning to reduce forage competition with domestic livestock, and sylvatic plague, an exotic disease catastrophic to prairie dogs (Cain and others, 1972; Hansen, 1988; Cully, 1993; Van Pelt, 1999; U.S. Fish and Wildlife Service, 2000; Cully and Williams, 2001; Antolin and others, 2002; Luce, 2003). Despite these potential conflicts and future challenges, identification of appropriate sites for black-footed ferret reintroduction has been ongoing for over two decades.

Although occupied prairie dog habitat has been significantly reduced since western settlement (Hoogland, 1995; Miller and Cully, 2001), it has been only in the last decade that the degree of both the quantity and quality of this loss relative to potential black-footed ferret recovery has been recognized. At present there may not be sufficient occupied prairie dog habitat in total in the historical ranges of the black-tailed prairie dog, white-tailed prairie dog, and Gunnison’s prairie dog, either in quantity or quality, for the black-footed ferret to be fully recovered, especially if black-footed ferret populations are to be broadly represented geographically as a precaution against depressant stochastic influences (M. Lockhart, written commun., 1999–2003).

The 1988 Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) set a downlisting goal for the species at 1,500 adults in 10 or more populations dispersed across its historical range, with no single population being less than 30 adults. Downlisting the species would move it from endangered to threatened status but would not represent complete recovery. Delisting the black-footed ferret through recovery sufficient to obviate its endangered status and permit its removal from the endangered species list (pursuant to the Endangered Species Act of 1973, as amended) would require even more recovery sites.

I suggest that it may be necessary to evaluate an order of magnitude more sites to achieve complete recovery and delisting, or 100 sites across the historical range of the species. These sites should be widely dispersed and represent the variety of habitats available, including different prairie dog species, ecological circumstances, disease prevalence, and the like. Since some sites may prove not to be usable for biological, social, or other reasons, or may not be successful, it will be necessary to consider many.

Plague is a confounding factor. Annual monitoring to document plague activity and the amount of habitat affected would assist prairie dog and black-footed ferret management. Continuing research on the mechanisms by which plague is spread, pretreatment of prairie dogs, and posttreatment of burrows to kill fleas and thus reduce the magnitude of an epizootic may allow practical management of the disease in the next 10 years. Meanwhile, maintaining spatial distribution of prairie dog complexes and isolated colonies over the entire range to act as reservoirs to replace prairie dogs lost to plague, as well as development of black-footed ferret reintroduction sites east of the plague line (in the plague-free area), will greatly assist in managing the impacts of the disease on prairie dogs.

In my opinion, data presented by Cully and Williams (2001) suggest that a fundamental change may be occurring in prairie dog ecology whereby some large colonies, especially those of black-tailed prairie dogs, may not persist when repeatedly challenged by plague. Persistence of only small colonies or complexes may have serious implications for black-footed ferret recovery. Extensive habitat will be necessary for reintroduction success, especially in the absence of management, and few large sites may persist at their full habitat capability in the face of repeated plague epizootics. On the other hand, recent surveys of white-tailed prairie dogs and black-footed ferrets in Shirley Basin, Wyo., indicate that these areas may have proportionately higher value than previously thought because both prairie dogs and black-footed ferrets have maintained significant populations in the presence of plague since monitoring was begun in 1991 (Luce, 2002; Grenier and others, 2004). In fact, both white-tailed prairie dog and black-footed ferret numbers increased despite more than 10 years of active plague (Grenier and others, 2004).

Status of Prairie Dog Conservation

Since black-footed ferret recovery and prairie dog management issues are closely tied, the future of the black-footed ferret essentially depends on developing effective management of black-tailed, white-tailed, and Gunnison’s prairie dogs. The Black-tailed Prairie Dog Conservation Team (later just the Prairie Dog Conservation Team), which includes representatives from 12 State wildlife agencies, has been working since 1998 to develop effective conservation for prairie dogs. The team first developed the Black-tailed Prairie Dog Conservation Assessment and Strategy (Van Pelt, 1999), which was followed by an addendum called the Black-tailed Prairie Dog Multi-State Conservation Plan (Luce, 2003), a guideline for development of State black-tailed prairie dog management plans. Black-tailed prairie dog management plans have been completed in Colorado, Kansas, Montana, New Mexico, North Dakota, Oklahoma, and Texas. Draft management plans are moving toward finalization in South Dakota and Wyoming. Arizona has a draft management plan and is currently evaluating black-tailed prairie dog reintroduction, while Nebraska does not expect to continue development of a management plan.

The Black-tailed Prairie Dog Multi-State Conservation Plan includes several provisions that are important to black-footed ferret recovery, two areas of which are of the greatest significance. First, the objectives for occupied area, shown in table 3, indicate a commitment on the part of a majority of the States with black-tailed prairie dogs to increase the occupied area from 631,127 ha to 685,946 ha by 2011 (Luce, 2003). Second, the Multi-State Conservation Plan sets other target objectives for the United States as follows:

1. Maintain at least the current occupied area of black-tailed prairie dog habitat in the two complexes greater than 2,025 ha that now occur on and adjacent to Conata Basin-Buffalo Gap National Grassland, S. Dak., and Thunder Basin National Grassland, Wyo.
2. Develop and maintain a minimum of nine additional complexes greater than 2,025 ha (with each State managing or contributing to at least one complex) by 2011. A State could contribute to a 2,025 ha complex along a State boundary by cooperating with the adjacent State to manage part of the complex. A similar agreement could be developed between a State and a Native American tribe.
3. Achieve and maintain at least 10 percent of total occupied habitat in colonies or complexes greater than 405 ha by 2011.

Table 3. Estimates of historical, current, gross, and suitable black-tailed prairie dog (*Cynomys ludovicianus*) habitat, and the 10-year minimum habitat objective (Luce, 2003). Native American tribes in Montana, South Dakota, and North Dakota will set an occupied-area objective independent of the States.

State	Historical potential habitat[1] (ha)	Current occupied habitat[2] (ha)	Gross habitat[3] (ha)	Suitable habitat[4] and minimum 10-year objective[5] (ha)
Arizona	2,854,090	0	2,854	1,861
Colorado	11,077,916	255,596	110,779	103,588
Kansas	14,513,206	52,861	61,039	60,181
Montana	24,479,316	36,450	120,401	97,349
Nebraska	14,594,350	32,400	59,430	55,588
New Mexico	15,803,686	24,300	39,148	35,288
North Dakota	4,473,334	8,303	44,733	40,723
Oklahoma	8,750,479	26,007	28,702	27,806
South Dakota	11,851,333	64,800	88,339	80,786
Texas	31,829,943	79,785	125,933	118,717
Wyoming	8,937,378	50,625	75,524	64,059
Total	149,165,031	631,127	756,882	685,946

[1] Historical potential habitat = total potential habitat (not occupied habitat) encompassed within the range of the black-tailed prairie dog (as mapped by Hall, 1981). See Luce (2003) for further explanation.

[2] Current occupied habitat = estimates provided by the individual States.

[3] Gross habitat = total area of core range × 0.01 + area of secondary range × 0.001. Core range was defined as Bailey Ecosections dominated by shortgrass prairie plants and having black-tailed prairie dogs on the list of native fauna. Secondary range was defined as Bailey Ecosections dominated by plants not associated with shortgrass prairie, or having historically suitable habitat but a current sociopolitical climate unfavorable for prairie dog management. See Luce (2003) for additional details.

[4] Suitable habitat = gross habitat minus habitat with >10% slope and habitats such as large bodies of water, badlands, wetlands, forests, or other features not used by prairie dogs. Agricultural lands were included if they met the slope criterion.

[5] Minimum 10-year objective = objective for minimum area of occupied prairie dog habitat in each State, and total for the 11 States, by 2011.

4. Maintain distribution across at least 75 percent of the counties in the historical range or at least 75 percent of the historical geographic distribution. Ten States currently meet this objective (Arizona does not since the black-tailed prairie dog was extirpated), and all but Nebraska and Arizona have black-tailed prairie dogs in 100 percent of the counties in the historical range. This objective addresses the need to maintain all prairie dog colonies, whatever the size or location, throughout the range. State management plans will deal directly with management of complexes and individual, isolated colonies.

Management strategies for black-tailed prairie dogs on tribal lands were prepared for the Intertribal Prairie Ecosystem Restoration Consortium in January 2002 (T. Vosburgh, oral commun., 2003). The goal is to develop and implement management programs for the conservation of prairie dog habitat. These management strategies were revised on February 4, 2002, following review and comment from participating tribes, the U.S. Fish and Wildlife Service, and the Interstate Coordinator for the 12-State Prairie Dog Conservation Team. The consortium convened twice in 2002 and is working with other groups and agencies to move prairie dog management and conservation forward. The tribes have drafted plans to ensure that prairie dog populations and habitat are maintained. The Lower Brule and Fort Belknap Indian Reservations have final prairie dog management plans in place, and draft plans have been prepared for the Fort Berthold, Northern Cheyenne, Crow Creek, and Rosebud Indian Reservations.

The States of Wyoming, Colorado, Utah, and Montana developed a conservation assessment for the white-tailed prairie dog in 2005 (Seglund and others, 2005a), as did the States of Arizona, New Mexico, Colorado, and Utah for the Gunnison's prairie dog (Seglund and others, 2005b). When a conservation strategy is developed for the Gunnison's prairie dog, complexes of colonies will be identified, and other sites with black-footed ferret reintroduction potential may thus become apparent.

Summary and Recommendations

The black-footed ferret recovery program has faced and overcome several obstacles to reach the point where it is today. Foremost were capture of the wild population at Meeteetse, Wyo., captive breeding, development of release strategies, and release site identification based on habitat suitability and other factors. Given that those obstacles to success were overcome, I believe that, at the present time, continued progress on black-footed ferret recovery depends upon identification and active management of additional reintroduction sites. To that end, I identify 70 sites in the historical range of the black-footed ferret that might meet the biological and habitat suitability requirements for reintroduction of black-footed ferrets within 3–10 years, contingent upon directed management emphasis, State and Federal agency management priorities, and, if on private land, landowner concurrence based on agreements or incentives.

The Black-footed Ferret Recovery Implementation Team and Prairie Dog Conservation Team are encouraged to:

- Cooperate closely with State and Federal agencies and eight tribal governments to move toward the targets set in the Black-tailed Prairie Dog Multi-State Conservation Plan and State and tribal management plans.
- Assist the White-tailed and Gunnison's Prairie Dog Working Groups to develop management plans for both species.
- Cooperate to evaluate the sites presented in this paper and develop strategies to begin management of as many sites as possible for black-footed ferret reintroduction within 10 years.
- Support and advance the High Plains Partnership landowner incentive program and/or other programs designed to bring about landowner participation in grassland species management.

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References Cited

Antolin, M.F., Gober, P., Luce, B., Biggins, D.E., Van Pelt, W.E., Seery, D.B., Lockhart, M., and Ball, M., 2002, The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation: Transactions of the North American Wildlife and Natural Resources Conference, v. 67, p. 104–127.

Biggins, D., 2003, Decline of a white-tailed prairie dog population near Meeteetse, Wyoming: Fort Collins, Colo., U.S. Geological Survey, Prairie Dog Research Update No. 8, 23 p.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Black-footed Ferret Advisory Team, 1990, A cooperative management plan for black-footed ferrets at Meeteetse: Cheyenne, Wyoming Game and Fish Department, 45 p.

Boschen, N.S., 1986, Black-footed ferret study in the Cisco Desert area of Utah, introductory report: Salt Lake City, Utah Division of Wildlife Resources, 21 p.

Cain, S.A., Kadlec, J.A., Allen, D.L., Cooley, R.A., Hornocker, M.G., Leopold, A.S., and Wagner, F.H., 1972, Predator control—1971: Ann Arbor, University of Michigan, Report to the Council on Environmental Quality and the Department of the Interior by the Advisory Committee, 207 p.

Chaplin, S.J., Ostlie, W.R., Schneider, R.E., and Kenney, J.S., 1996, A multiple-scale approach to conservation planning in the Great Plains, *in* Samson, F.B., and Knopf, F.L., eds., Prairie conservation—preserving North America's most endangered ecosystem: Washington, D.C., Island Press, p. 187–201.

Clark, T.W., 1986, Some guidelines for management of the black-footed ferret: Great Basin Naturalist Memoirs No. 8, p. 160–168.

Clark, T.W., and Campbell, T.M., III, 1981, Additional black-footed ferret (*Mustela nigripes*) reports from Wyoming: Great Basin Naturalist, v. 41, p. 360–361.

Colorado Division of Wildlife, 2003, Conservation plan for grassland species in Colorado: Denver, Colorado Division of Wildlife, 38 p.

Conway, C.J., 1989, Evaluation of potential black-footed ferret reintroduction sites in Wyoming: Report prepared for the Wyoming Game and Fish Department, 10 p.

Cranney, S.J., and Day, K.S., 1994, 1993 prairie dog density surveys in the Diamond Mountain Resource Area: Vernal, Utah Division of Wildlife, Northeast Region, 8 p.

Cully, J.F., and Williams, E.S., 2001, Interspecific comparisons of sylvatic plague in prairie dogs: Journal of Mammalogy, v. 82, p. 894–905.

Cully, J.F., Jr., 1993, Plague, prairie dogs, and black-footed ferrets, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 38–49.

EDAW, Inc., 2000, Black-tailed prairie dog study of eastern Colorado: Report to the Colorado Department of Natural Resources, Denver, 31 p.

Ernst, A.E., 2001, Changes in black-tailed prairie dog towns on the Texas Panhandle determined by a geographic information system: Lubbock, Texas Tech University, M.S. thesis, 99 p.

Forrest, S.C., Clark, T.W., Richardson, L., and Campbell, T.M., III, 1985, Black-footed ferret habitat—some management and reintroduction considerations: Cheyenne, Wyoming BLM Wildlife Technical Bulletin No. 2, 49 p.

Grenier, M., Carpenter, A., Martin, M., Purcell, M., and Stephens, J., 2003, Black-footed ferret habitat evaluation of historical white-tailed prairie dog complexes in Wyoming, completion report, April 2003: Lander, Wyoming Game and Fish Department, 19 p.

Grenier, M., Van Fleet, L., and Oakleaf, B., 2004, Spotlighting for free-ranging black-footed ferrets in the Shirley Basin/Medicine Bow Management Area, Wyoming, *in* Cerovski, A., ed., Threatened, endangered, and nongame bird and mammal investigations, annual completion report: Lander, Wyoming Game and Fish Department, p. 19–35.

Hall, E.R., 1981, The mammals of North America (2d ed.): New York, John Wiley, 1,181 p.

Hansen, R.M., 1988, A chronology of prairie dog control operations and related developments in South Dakota, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: USDA Forest Service, General Technical Report RM-154, p. 121–122.

Hnilicka, P., and Luce, B., 1992, Habitat evaluation of the Shirley Basin/Medicine Bow black-footed ferret management area and selection of criterion for the premier reintroduction site, *in* Oakleaf, B., Luce, B., Thorne, E.T., and Torbit, S., eds., 1991 Annual completion report—black-footed ferret reintroduction, Shirley Basin: Lander, Wyoming Game and Fish Department, p. 39–51.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing mammal: Chicago, University of Chicago Press, 557 p.

Johnson, K., Neville, T., and Price, L., 2003, Remote sensing survey of black-tailed prairie dog towns in the historical New Mexico range: Albuquerque, New Mexico Natural Heritage Program, University of New Mexico, 28 p.

Kansas Black-tailed Prairie Dog Working Group, 2002, Kansas black-tailed prairie dog conservation and management plan: Pratt, Kansas Black-tailed Prairie Dog Working Group, 29 p.

Knowles, C.J., 2003, Status of the black-tailed prairie dog in North Dakota: Report prepared for the North Dakota Game and Fish Department, Bismarck, 56 p.

Lair, P., and Mecham, J., 1991, Black-footed ferret restoration evaluation/prairie dog status: Federal Aid report to the Texas Parks and Wildlife Department, WNM-KH-U, job no. 70, Aug. 31, 1991, 16 p.

Lomolino, M.V., and Smith, G.A., 2001, Dynamic biogeography of prairie dog (*Cynomys ludovicianus*) towns near the edge of their range: Journal of Mammalogy, v. 82, p. 937–945.

Lomolino, M.V., Smith, G.M., and Vidal, V., 2002, Long-term persistence of prairie dog towns—insights for designing networks of prairie reserves: Biological Conservation, v. 115, p. 111–120.

Luce, R.J., 2002, Black-footed ferret release site monitoring in Shirley Basin, Wyoming, *in* Brand, C.J., ed., Proceedings of an American Southwest Workshop—Landscape ecology of plague in the American Southwest, September 19–20, 2000, Fort Collins, Colo., p. 15.

Luce, R.J., 2003, A multi-state conservation plan for the black-tailed prairie dog, *Cynomys ludovicianus*, in the United States—an addendum to the Black-tailed Prairie Dog Conservation Assessment and Strategy, November 3, 1999: Sierra Vista, Ariz., Prairie Dog Conservation Team, 79 p.

Martin, D., and Luce, B., 1990, Black-footed ferret surveys, *in* 1990 Nongame program annual completion report: Lander, Wyoming Game and Fish Department, p. 30–38.

Miller, B., Reading, R.P., Forrest, S., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Miller, S.D., and Cully, J.F., Jr., 2001, Conservation of black-tailed prairie dogs (*Cynomys ludovicianus*): Journal of Mammalogy, v. 82, p. 894–905.

Montana Prairie Dog Working Group, 2002, Conservation plan for black-tailed and white-tailed prairie dogs in Montana: Helena, Montana Prairie Dog Working Group, 51 p.

Orabona-Cerovski, A., 1991, Habitat characteristics, population dynamics, and behavioral interactions of white-tailed prairie dogs in Shirley Basin, Wyoming: Laramie, University of Wyoming, M.S. thesis, 182 p.

Parrish, T.L., and Luce, B., 1990, Evaluation of potential black-footed ferret reintroduction sites in Wyoming: Laramie, Wyoming Cooperative Fish and Wildlife Research Unit and Wyoming Game and Fish Department, 14 p.

Seglund, A.E., Ernst, A.E., Grenier, M., Luce, B., Puchniak, A., and Schnurr, P., 2005a, White-tailed prairie dog conservation assessment: Laramie, Wyo., Western Association of Fish and Wildlife Agencies, 138 p.

Seglund, A.E., Ernst, A.E., and O'Neill, D., 2005b, Gunnison's prairie dog conservation assessment: Laramie, Wyo., Western Association of Fish and Wildlife Agencies, 87 p.

South Dakota Prairie Dog Work Group, 2001, Draft South Dakota black-tailed prairie dog management plan: Pierre, South Dakota Department of Game, Fish, and Parks, 77 p.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

U.S. Fish and Wildlife Service, 2000, 12-month finding for a petition to list the black-tailed prairie dog as threatened: Federal Register, v. 65, p. 5476–5488.

Vanderhoof, J.L., and Robel, R.J., 1992, Numbers and extent of black-tailed prairie dog towns in western Kansas. Final report—prairie dog population monitoring, habitat, attributes, and behavior: Contract no. 221, Kansas Department of Wildlife and Parks, 43 p.

Vanderhoof, J.L., and Robel, R.J., 1994, Numbers and extent of black-tailed prairie dog towns in Kansas: Transactions of the Kansas Academy of Science, v. 97, p. 36–43.

Van Pelt, W.E., 1999, The black-tailed prairie dog conservation assessment and strategy: Phoenix, Arizona Game and Fish Department, 55 p.

Wagner, D.M., and Drickamer, C., 2002, Distribution, habitat use, and plague in Gunnison's prairie dogs in Arizona: Heritage Grant I20009, report to the Arizona Game and Fish Department, 50 p.

A Habitat-based Technique To Allocate Black-footed Ferret Recovery Among Jurisdictional Entities

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Abstract

We offer a technique to allocate a hypothetical black-footed ferret (*Mustela nigripes*) recovery goal in an equitable fashion across the historical range of ferrets. A geographic information system (GIS) was used to predict the distribution of prairie dog (*Cynomys* spp.) habitat where the black-footed ferret historically occurred. Proportions of predicted habitat by jurisdictional entity provided a foundation to allocate a hypothetical delisting of the black-footed ferret. Subject to modification, this technique is presented as an example to bring long-term ferret recovery into finer focus at a national scale. In addition, we offer this technique to encourage a broader assessment of future reintroduction sites, to inspire creative thinking on how recovery goals could be allocated across the historical range, and to motivate collaborative efforts among Federal and State agencies, conservation groups, and private landowners to increase the likelihood of successful recovery of the black-footed ferret.

Keywords: black-footed ferret, *Cynomys*, geographic information system, GIS, *Mustela nigripes*, prairie dog, predicted habitat model, recovery

Introduction

The ultimate goal of the Endangered Species Act is recovery and subsequent preservation of threatened or endangered species (U.S. Fish and Wildlife Service, 2002a). Achievement of this goal can be defined in terms of downlisting, which is the reclassification of a species from endangered to threatened status, or delisting, which is the removal of a species from the Federal List of Endangered and Threatened Wildlife and Plants (Cole, 1989; U.S. Fish and Wildlife Service, 2002a). Downlisting and delisting result from successful recovery efforts; delisting occurs when protection of a species is no longer deemed necessary. To coordinate recovery efforts among Federal, State, and local agencies, the U.S. Fish and Wildlife Service prepares recovery plans that outline necessary procedures to achieve downlisting and delisting. Recovery plans identify specific tasks aimed at making a species a viable, self-sustaining component of its ecosystem (Cole, 1989; U.S. Fish and Wildlife Service, 2002b).

The first recovery plan for the critically endangered black-footed ferret (*Mustela nigripes*) was approved in 1978. At that time, no ferrets were known to exist in the wild (U.S. Fish and Wildlife Service, 1988; Cole, 1989). The subsequent discovery of a wild population of ferrets in Wyoming necessitated revision of the recovery plan. The main revision was a shift in management emphasis from free-ranging ferret populations to captive breeding and reintroduction (Biggins and Thorne, 1994). The revised recovery plan (U.S. Fish and Wildlife Service, 1988) placed the ferret program in a national scope and outlined steps "to ensure immediate survival of the black-footed ferret by: (1) increasing the captive population of black-footed ferrets to a census size of 200 breeding adults by 1991; (2) establishing a pre-breeding census population of 1,500 free-ranging black-footed ferret breeding adults in 10 or more populations with no fewer than 30 breeding adults in any population by the year 2010; and (3) encourage the widest possible distribution of reintroduced black-footed ferret populations" (U.S. Fish and Wildlife Service, 1988, p. 19).

As stated in the third step in the recovery plan, reintroduction of ferrets should be considered in the context of their historical geographic range. Selection of reintroduction sites should be based on several biological considerations, including the vulnerability of ferrets to demographic stochasticity (survival of population subgroups); environmental stochasticity (diseases, changes in predator densities); and genetic stochasticity (effects of inbreeding and loss of genetic variation through drift) (Shaffer, 1981; Groves and Clark, 1986; Clark, 1994). To be successful, however, black-footed ferret recovery must also involve more than biological considerations (Kleiman and others, 2000), and a variety of issues, including availability and ownership of potential habitat, should be considered when selecting reintroduction sites.

To date, selection of reintroduction sites has focused on identifying, protecting, and developing the most promising and

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largest reintroduction locations; however, large reintroduction sites may not be developed as rapidly as needed, and availability of these sites should not limit overall ferret recovery (Clark, 1994). New sites need to be identified, and maintenance of a few large sites should not necessarily preclude other, smaller recovery areas. To contribute to the overall recovery effort and to fulfill State recovery objectives, a strategy that incorporates recovery areas of various sizes would maximize the potential to secure ferret populations in the wild (U.S. Fish and Wildlife Service, 1988).

Additional challenges in ferret recovery include successful ferret reintroduction and effective long-term management of the sites (Reading and Miller, 1994). Selection of potential reintroduction sites is problematic and controversial and has suffered from disagreements among multiple interest groups, conflicting objectives, biological uncertainty, sociopolitical constraints, and intense public scrutiny (Maguire and others, 1988). Given these challenges, field biologists, veterinarians, and administrators representing Federal, State, and private agencies must provide a means by which to allocate ferret recovery in an equitable fashion. Equitable allocation will encourage participation by all entities and help place long-term ferret recovery in a national scope. To assist in meeting these challenges, we offer a habitat-based technique to allocate reintroduction efforts among jurisdictional entities. This technique is based on quantifying the relative amount of potential habitat across the geographic range. We offer this technique only as a test case to help bring long-term ferret recovery into finer focus at the national scale. Further, our technique will potentially broaden current assessments of future reintroduction sites and encourage cooperation across the extended network of people involved in the survival of the black-footed ferret.

Methods

Digital Data Layers

Recent advances in computer-aided mapping, combined with accessibility of geographic information system (GIS) data sets, enable production of digital maps depicting distributions of predicted habitat at a spatially detailed, landscape scale. Historical black-footed ferret specimens were recorded in association with three species of prairie dogs (*Cynomys* spp.), including the black-tailed prairie dog (*C. ludovicianus*), white-tailed prairie dog (*C. leucurus*), and Gunnison's prairie dog (*C. gunnisoni*) (Anderson and others, 1986). Further, black-footed ferret habitat is often defined in terms of prairie dog colonies. Thus, we created predictive habitat distribution models for the three species of prairie dogs. We defined and restricted the geographic area used in the predictive models by using the comprehensive prairie dog range maps as described by Hall (1981). These maps characterize the extremes of the area where prairie dog species were found historically and incorporate all known specimen records, including marginal habitats and disjunct populations. The range distribution maps provided by Hall (1981) were scanned with a desktop scanning device at 800 dots per inch. The digital images were saved in a tagged image file format to provide baseline GIS coverages. These images were registered to geographic coordinates, and distribution boundaries were digitized for each prairie dog species. We did not include the Utah prairie dog (*C. parvidens*) because evidence suggests that black-footed ferrets were not associated with this species (Anderson and others, 1986).

Collection records demonstrate that ferrets, until the first decades of the 20th century, were distributed over 40 million ha in 12 States and 2 Canadian Provinces (Anderson and others, 1986; Clark, 1986, 1987). County jurisdictional boundaries were acquired from the National Atlas of the United States® (http://www.nationalatlas.gov), imported into ArcGIS® 8.3 software (Environmental Systems Research Institute, Inc., Redlands, Calif.), and dissolved by State attributes, producing boundaries at a scale of 1:100,000 for the 12 States in which the black-footed ferret historically occurred.

Digital data sets depicting landscape attributes were chosen based on the availability and uniformity of data across the geographic range. We used the U.S. Geological Survey (USGS) National Land Cover Dataset (NLCD; http://landcover.usgs.gov/natllandcover.asp) to provide an estimate of current land cover. This data set depicts generalized land cover categories labeled agriculture, urban areas, forests, wetlands, grasslands, and shrublands with a 30-m spatial resolution. The NLCD was created from Landsat 5 Thematic Mapper satellite imagery digitally captured in 1992, produced by the Earth Resources Observation System Data Center. The NLCD was downloaded in complete State sections, which included a 300-m (10-pixel) buffer added to each outer State boundary. The data were then imported into ERDAS IMAGINE® 8.6 (Leica Geosystems Geospatial Imaging, LLC, Norcross, Ga.) and projected into a common coordinate system. Each State was clipped to the individual jurisdictional boundaries.

We used the USGS National Elevation Dataset (NED) to provide continuous, seamless elevation information at a 30-m spatial resolution. We downloaded the NED (http://ned.usgs.gov) in individual 1:250,000 quadrangles. The individual quadrangles were then map-joined to create one complete data layer for each State. Each data layer, as with all GIS data used in the model, was projected to a common coordinate system (Albers Equal Area projection). This projection is used in the United States and other countries that have a larger east-west than north-south extent because it preserves the area of the displayed features over the entire map with the same proportional relationship as the actual geographic areas they represent (Kennedy and Kopp, 2000). The individual data sets were then clipped to the State jurisdictional boundaries.

Predicted Habitat Models

We created digital models of predicted prairie dog habitat based on a set of landscape attributes and wildlife-habitat relationships. The wildlife-habitat relationships were based on attributes important in defining prairie dog habitat, such as land cover and topographic gradient (Koford, 1958; Clippinger, 1989). Generalized land cover categories considered suitable prairie dog habitat were grassland, shrubland, small grains, row crops, and pastures. Land cover types considered unsuitable were forests, water, and snow. Residential, wetland, and fallow land cover types may provide some prairie dog habitat; however, we considered these contributions minimal and placed these land cover types in the unsuitable category.

Topographic gradient was an additional landscape attribute used to predict prairie dog habitat. We used an algorithm in ERDAS IMAGINE 8.6 to derive percent slope from the NED. Slopes of 0–10 percent were considered suitable habitat. Although prairie dogs may occur on slopes greater than 10 percent, black-tailed prairie dogs usually build on slopes of less than 10 percent (Koford, 1958; Dalstead and others, 1981; Clippinger, 1989). Therefore, the remaining slope categories (11 percent and greater) were considered unsuitable habitat for all prairie dog species.

The Spatial Modeler module of ERDAS IMAGINE 8.6 was used to produce the individual predicted habitat models for each State. We used the additive overlay technique, which combined each individual data layer as an equally weighted component in the model. Although this process is referred to as additive, the file produced depicts the specific combination of the appropriate land cover and slope attributes selected as suitable prairie dog habitat. The predicted models for each State were then clipped to the individual range boundaries and merged into one complete data set. The result was a predicted habitat model for each prairie dog species.

The final step in modeling predicted habitat was removal of small, isolated tracts. Our models were produced at a 30-m spatial resolution, which we considered to be below the minimum habitat area required for black-footed ferrets. Minimum habitat area can be defined as the minimum amount of contiguous habitat that is required before an area will be occupied by a species (Clippinger, 1989). Because the different prairie dogs species afford different ferret carrying capacities, the size of suitable reintroduction areas ultimately depends on densities of prey. For example, ferrets have been shown to occur at densities of one adult black-footed ferret per 40–60 ha in white-tailed prairie dog colonies (Forrest and others, 1985; Richardson and others, 1986; U.S. Fish and Wildlife Service, 1988). Hillman and others (1979) found that 6 of 11 observed ferret litters occupied black-tailed prairie dog colonies greater than 40 ha. Further, black-tailed prairie dogs tend to be more gregarious and thus occur in more dense populations. Therefore, the minimum area of black-tailed prairie dog colonies that can support ferrets may be smaller than that for other prairie dog species (Clark, 1994).

We removed patches that were below the minimum size suitable for black-footed ferret survival in each habitat model with the Clump and Eliminate commands in ERDAS IMAGINE. We filtered predicted habitat based on the minimum area suitable for black-footed ferret survival. We used a minimum patch size of 40 ha in the black-tailed prairie dog range, 60 ha in the Gunnison's prairie dog range, and 80 ha in the white-tailed prairie dog range.

Although the ability of various habitats to support populations of a given size will only be known from the results of reintroductions, at present it appears that large complexes are necessary for viable ferret populations (U.S. Fish and Wildlife Service, 1988). The minimum areas we chose may be reasonable based on available bioenergetic and behavioral information, however, and we offer them as working hypotheses in presenting our methodology for allocating ferret recovery.

Ferret Allocation

The 1988 recovery plan deferred specification of a delisting population size pending outcomes of reintroductions and accumulation of additional management experience (U.S. Fish and Wildlife Service, 1988). We offer a hypothetical delisting population size of 15,000 ferrets, an order of magnitude larger than the downlisting objective specified in the 1988 recovery plan. We chose this value based on several lines of reasoning. First, large prairie dog colonies such as those currently used for reintroductions may be scarce (Dobson and Lyles, 2000). Additional, smaller populations may be necessary to meet any delisting objective. Second, a larger number of smaller populations may help protect against catastrophic events (e.g., disease outbreaks) that can decimate entire populations (Forrest and others, 1988). Third, fossil evidence supports the hypothesis that black-footed ferrets may have been more common throughout the historical range (Linder and others, 1972; Choate and others, 1982; Hubbard and Schmitt, 1984; Anderson and others, 1986).

Although the majority of habitat occurs in the black-tailed prairie dog range, we suggest larger than proportional allocations of black-footed ferrets in the white-tailed and Gunnison's prairie dog ranges. We suggest 8,625 ferrets (57.5 percent) allocated to the black-tailed prairie dog range; 3,375 ferrets (22.5 percent) to the Gunnison's prairie dog range; and 3,000 ferrets (20 percent) to the white-tailed prairie dog range. To equitably divide ferret recovery across jurisdictional entities, we calculated the total amount of predicted habitat in the individual prairie dog ranges, calculated the percent of predicted habitat in each State, and then used those percentages to apportion black-footed ferrets by State and by prairie dog species.

Results and Discussion

Black-tailed Prairie Dog

Using the model described above, we calculated about 128.9 million ha of predicted habitat in the black-tailed prairie dog range (table 1), or about 71 percent of the range distribution as described by Hall (1981). The largest amount of predicted habitat occurred in Texas and encompassed over 29.2 million ha. New Mexico provided the second largest amount of predicted habitat with ~16.0 million ha. Nebraska, Kansas, and Montana had similar amounts of predicted habitat, with approximately 14 million ha each. North Dakota and Arizona, both considered range extremes, had the smallest estimate of predicted habitat with ~3.5 million ha and ~1.5 million ha, respectively. Texas was allocated 1,957 individual black-footed ferrets, and New Mexico was allocated 1,072 ferrets. South Dakota, where the last known extant populations of ferrets occurred in the black-tailed prairie dog range, was allocated 746 black-footed ferrets, and Wyoming was

Table 1. Amount of predicted habitat by prairie dog (*Cynomys*) species and jurisdictional entity, and resulting black-footed ferret (*Mustela nigripes*) allocations based on the hypothetical delisting objective of 15,000 individuals.

State	Predicted habitat (ha)	Percent of predicted habitat within each jurisdictional entity	Number of ferrets allocated	Minimum habitat required (ha)	Minimum habitat as a percent of total
		Black-tailed prairie dog (*C. ludovicianus*)			
Arizona	1,484,257	1.2	99	3,960	
Colorado	9,870,127	7.7	660	26,400	
Kansas	13,977,156	10.8	935	37,400	
Montana	13,719,492	10.6	918	36,720	
Nebraska	14,660,668	11.4	981	39,240	
New Mexico	16,024,114	12.4	1,072	42,880	
North Dakota	3,520,025	2.7	236	9,440	
Oklahoma	7,764,139	6.0	520	20,800	
South Dakota	11,145,988	8.6	746	29,840	
Texas	29,248,634	22.7	1,957	78,280	
Wyoming	7,486,045	5.8	501	20,040	
Total	128,900,645	100.0	8,625	345,000	0.27
		Gunnison's prairie dog (*C. gunnisoni*)			
Arizona	5,338,155	39.4	1,331	79,860	
Colorado	2,206,766	16.3	551	33,060	
New Mexico	5,505,857	40.7	1,373	82,380	
Utah	482,473	3.6	120	7,200	
Total	13,533,251	100.0	3,375	202,500	1.50
		White-tailed prairie dog (*C. leucurus*)			
Colorado	934,483	8.9	268	21,440	
Montana	53,308	0.5	15	1,200	
Utah	1,075,817	10.3	309	24,720	
Wyoming	8,394,910	80.3	2,408	192,640	
Total	10,458,518	100.0	3,000	240,000	2.29

allocated 501. The State with the lowest ferret allocation was Arizona.

Based on our calculations (table 1), the minimum amount of habitat needed in the range of the black-tailed prairie dog was about 345,000 ha. Texas, with 23 percent of the predicted habitat, required a minimum of ~78,000 ha, and New Mexico required ~43,000 ha. Arizona could contribute ~4,000 ha. Overall, the minimum amount of habitat needed to achieve the hypothetical delisting objective was less than 1 percent of the total predicted habitat.

The amount of predicted habitat was calculated from input variables based on our model. We recognize that different definitions of suitable land cover could result in different amounts of predicted habitat and different ferret allocations. For example, we included agricultural land in our model based on the recognition that large areas of historically suitable prairie dog habitat were converted to cropland after settlement because prairie dogs prefer deep, relatively level soils—the same land preferred for agricultural development (Choate and others, 1982; Clark, 1986). Although we do not assume that land under current cultivation practices would be converted back to rangeland solely to provide black-footed ferret habitat, some agricultural practices may be compatible with black-footed ferret and prairie dog management, provided that prairie dogs can be tolerated (U.S. Fish and Wildlife Service, 1988). Overall, the agriculture class was approximately 44.7 million ha or 34 percent of the predicted habitat in the black-tailed prairie dog range. Oklahoma and Kansas had the largest proportions of agriculture, with more than 52 percent of the area under cultivation. In New Mexico, agriculture totaled over 48 percent of the area.

Gunnison's Prairie Dog

The amount of predicted habitat in the Gunnison's prairie dog range was over 13.5 million ha or 40 percent of the range distribution as described by Hall (1981). New Mexico had ~5.5 million ha of predicted habitat, followed closely by Arizona with ~5.3 million ha. Colorado had ~2.2 million ha of predicted habitat and Utah ~482,000 ha (table 1).

Based on our calculations, New Mexico and Arizona were allocated a similar number of black-footed ferrets, approximately 1,350 individuals. Colorado and Utah combined were allocated 671 ferrets. Our results indicate that the minimum amount of habitat needed to achieve the hypothetical ferret recovery goal was 1.5 percent of the total predicted habitat in the Gunnison's prairie dog range.

Unlike the black-tailed prairie dog range, inclusion of the agriculture land cover class did not have much impact in the Gunnison's prairie dog range. Only 5 percent of the area was estimated to be in agriculture; however, additional information, as it becomes available at a regional scale, might improve the model. For example, soil type, soil depth, and rock ground cover are important variables in defining Gunnison's prairie dog habitat (Wagner and Drickamer, 2004). These variables should be included in the model when the spatial data become available.

White-tailed Prairie Dog

White-tailed prairie dogs afforded the least amount of predicted habitat, ~10.5 million ha or 45 percent of the range distribution as described by Hall (1981). The majority of predicted habitat in the white-tailed prairie dog range occurred in Wyoming, which had over 8.3 million ha. Montana was estimated to have less than 1 percent of the total predicted habitat (table 1).

Based on our estimates (table 1), Wyoming could host 2,408 black-footed ferrets, Utah 309, Colorado 268, and Montana 15. Overall, in the white-tailed prairie dog range, the minimum amount of habitat needed to reach the hypothetical black-footed ferret recovery goal was 240,000 ha, with Wyoming contributing most of the potential habitat. The minimum amount of habitat estimated to achieve our hypothetical delisting objective was 2.3 percent of the total predicted available habitat.

As with the Gunnison's prairie dog predicted model, inclusion of agriculture did not strongly affect the outcome for white-tailed prairie dogs, with only 7 percent of the area classified in the agriculture land cover type; however, the white-tailed prairie dog model could be improved with more detailed land cover information. For example, the NLCD shrubland cover class may be too general to define white-tailed prairie dog habitat. Although white-tailed prairie dogs occur in shrubland habitats, shrub height and density (Collins and Lichvar, 1986) may be better predictive variables.

Distribution of Resources

Based on our model, Wyoming received the largest allocation of black-footed ferrets with approximately 2,909 individuals. New Mexico was allocated 2,445 individuals and Texas 1,957. The total amount of predicted habitat across all prairie dog species was 152.9 million ha. We calculated a minimum of 787,500 ha of habitat needed to attain the hypothetical delisting of the black-footed ferret, or less than 1 percent of the potential available habitat. Our results support the conclusion in the 1988 recovery plan that sufficient habitat to meet downlisting is less than 0.1 percent (75,000–100,000 ha) of western rangelands (U.S. Fish and Wildlife Service, 1988).

Conclusion

Our technique has several underlying assumptions. The principal assumption is that all prairie dog habitat is suitable black-footed ferret habitat. We recognize that black-footed ferret habitat is more restricted, requiring complex spatial configurations of prairie dog colonies, specific distances between those colonies, and substantial prairie dog densities (Stromberg and others, 1983; Houston and others, 1986; Biggins, Lockhart, and Godbey, this volume). Another assumption of our technique is that land cover data identified from modern remote sensing platforms can reasonably predict prairie dog habitat. Nevertheless, we offer this technique as a test case and encourage modifications and refinements. Future efforts should consider using a larger variety of input variables with more locally specific information, different classifications of land cover or slope categories, and greater spatial resolution.

Our technique (or refinements of it) could be used to allocate black-footed ferret recovery across jurisdictional entities. This technique may help place long-term black-footed ferret recovery into a national scope based on equitable contributions among those entities. In so doing we hope to inspire creative thinking on how specific recovery goals might be allocated across the historical range. We hope to motivate the collaborative effort among Federal and State agencies, conservation groups, and private landowners that will be needed to turn the black-footed ferret back from the brink of extinction (Cole, 1989; Reading and Miller, 1994).

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References Cited

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Biggins, D.E., and Thorne, E.T., 1994, Conservation management case studies, *in* Meffe, G.K., and Carroll, C.R., eds., Principles of conservation biology: Sunderland, Mass., Sinauer Associates, Inc., p. 368–374.

Choate, J.R., Boggess, E.K., and Henderson, F.R., 1982, History and status of the black-footed ferret in Kansas: Transactions of the Kansas Academy of Science, v. 85, p. 121–132.

Clark, T.W., 1986, Black-footed ferret—ghost of the prairie: Animal Kingdom, v. 89, p. 38–48.

Clark, T.W., 1987, Black-footed ferret recovery—a progress report: Conservation Biology, v. 1, p. 8–11.

Clark, T.W., 1994, Restoration of the endangered black-footed ferret—a twenty-year overview, *in* Bowles, M.L., and Whelan, C.J., eds., Restoration of endangered species—conceptual issues, planning and implementation: United Kingdom, University of Cambridge Press, p. 272–297.

Clippinger, N.W., 1989, Habitat suitability index models—black-tailed prairie dog: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 82(10.156), 21 p.

Cole, B.P., 1989, Recovery planning for endangered and threatened species, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 201–209.

Collins, E.I., and Lichvar, R.W., 1986, Vegetation inventory of current and historic black-footed ferret habitat in Wyoming: Great Basin Naturalist Memoirs No. 8, p. 85–93.

Dalstead, K.J., Sather-Blair, S., Worchester, B.K., and Klukas, R., 1981, Application of remote sensing to prairie dog management: Journal of Range Management, v. 34, p. 218–223.

Dobson, A., and Lyles, A., 2000, Black-footed ferret recovery: Science, v. 288, p. 985–988.

Forrest, S., Clark, T.W., Biggins, D., Richardson, L., Fagerstone, K., and Campbell, T.M., III, 1985, Life history characteristics of the genus *Mustela*, with special reference to the black-footed ferret, *Mustela nigripes*, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 23.1–23.14.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Groves, C.R., and Clark, T.W., 1986, Determining minimum population size for recovery of the black-footed ferret: Great Basin Naturalist Memoirs No. 8, p. 150–159.

Hall, E.R., 1981, The mammals of North America (2d ed.): New York, John Wiley, 1,181 p.

Hillman, C.N., Linder, R.L., and Dahlgren, R.B., 1979, Prairie dog distributions in areas inhabited by black-footed ferrets: American Midland Naturalist, v. 102, p. 185–187.

Houston, B.R., Clark, T.W., and Minta, S.C., 1986, Habitat suitability index model for the black-footed ferret—a method to locate transplant sites: Great Basin Naturalist Memoirs No. 8, p. 99–114.

Hubbard, J.P., and Schmitt, C.G., 1984, The black-footed ferret in New Mexico: Santa Fe, N. Mex., Bureau of Land Management, 118 p.

Kennedy, M., and Kopp, S., 2000, Understanding map projections—GIS by ESRI: Redlands, Calif., Environmental Systems Research Institute, Inc., 110 p.

Kleiman, D.G., Reading, R.P., Miller, B.J., Clark, T.W., Scott, J.M., Robinson, J., Wallace, R.L., Cabin, R.J., and Felleman, F., 2000, Improving the evaluation of conservation programs: Conservation Biology, v. 14, p. 356–365.

Koford, C.B., 1958, Prairie dogs, whitefaces, and blue grama: Wildlife Monographs, no. 3, 78 p.

Linder, R.L., Dahlgren, R.B., and Hillman, C.N., 1972, Black-footed ferret-prairie dog interrelationships, *in* Symposium on rare and endangered wildlife of the Southwestern United States: Santa Fe, New Mexico Department of Game and Fish, p. 22–37.

Maguire, L.A., Clark, T.W., Crete, R., Cada, J., Groves, C., Shaffer, M.L., and Seal, U.S., 1988, Black-footed ferret recovery in Montana—a decision analysis: Wildlife Society Bulletin, v. 16, p. 111–120.

Reading, R.P., and Miller, B.J., 1994, The black-footed ferret recovery program—unmasking professional and organizational weaknesses, *in* Clark, T.W., Reading, R., and Clarke, A., eds., Endangered species recovery—finding the lessons, improving the process: Washington, D.C., Island Press, p. 73–100.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1986, Black-footed ferret recovery—a discussion of some options and considerations: Great Basin Naturalist Memoirs No. 8, p. 169–184.

Shaffer, M.L., 1981, Minimum population sizes for species conservation: BioScience, v. 31, p. 131–134.

Stromberg, M.R., Rayburn, R.L., and Clark, T.W., 1983, Black-footed ferret prey requirements—an energy balance estimate: Journal of Wildlife Management, v. 47, p. 67–73.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

U.S. Fish and Wildlife Service, 2002a, Delisting a species—Section 4 of the Endangered Species Act: Arlington, Va., U.S. Fish and Wildlife Service, 2 p.

U.S. Fish and Wildlife Service, 2002b, Endangered species recovery program—frequently asked questions: Arlington, Va., U.S. Fish and Wildlife Service, 2 p.

Wagner, D.M., and Drickamer, L.C., 2004, Abiotic habitat correlates of Gunnison's prairie dog in Arizona: Journal of Wildlife Management, v. 68, p. 188–197.

Habitat Restoration and Management

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Abstract

Black-footed ferrets (*Mustela nigripes*) historically occupied colonies of three prairie dog (*Cynomys*) species—Gunnison's (*C. gunnisoni*), white-tailed (*C. leucurus*), and black-tailed (*C. ludovicianus*)—more or less throughout their ranges. Historical declines in the abundance of ferret habitat (prairie dog colonies) resulted from poisoning of prairie dogs, sylvatic plague, conversion of habitat to agriculture, and changes in grazing practices to benefit mid-height and tall grasses. Prairie dog restoration often involves translocating prairie dogs into vacant habitat and managing vegetation to enhance colony growth. Sites for reestablishment should be selected with attention to ecological suitability, level of plague risk, return on economic investment in restoration and management, and social acceptability. Plague, conventional grazing and farming practices, and hostility of land managers toward prairie dogs can depress rates of restoration, but incentives may help overcome these obstacles. Two case histories illustrate restoration and management of black-tailed prairie dogs in two grassland types—mixed-grass and shortgrass. Options for expanding ferret habitat restoration and management opportunities include using small prairie dog complexes for ferret releases, introducing more intensive grazing to benefit black-tailed prairie dogs in taller grasslands, and reclaiming retired farmlands with shortgrass species beneficial to prairie dogs.

Keywords: black-footed ferret, *Cynomys* spp., habitat, management, *Mustela nigripes*, prairie dog, restoration

Introduction

Black-footed ferrets (*Mustela nigripes*) require populations of prairie dogs (*Cynomys* spp.) for sustained existence in the wild. Historical distribution records of ferrets coincide closely (though not exactly) with the presence of prairie dog colonies and the known historical ranges of three prairie dog species—black-tailed (*C. ludovicianus*), white-tailed (*C. leucurus*), and Gunnison's (*C. gunnisoni*). Ferrets collected outside prairie dog colonies or ranges could have come from ferret populations within colonies (Hubbard and Schmitt, 1984; Anderson and others, 1986). Efforts to recover ferrets proceed under the assumption that wild populations cannot long survive without prairie dogs (U.S. Fish and Wildlife Service, 1988).

Ferret habitat restoration thus implies restoration and management of prairie dogs, which of course requires suitable prairie dog habitat. Many landscapes historically occupied by black-tailed, white-tailed, or Gunnison's prairie dogs have been changed by conversion to agriculture, alterations in large herbivore abundance, or increases in woody vegetation. Singly or in combination, these changes have altered habitat suitability for prairie dogs (U.S. Fish and Wildlife Service, 2000; Knowles, 2002). Thus, habitat restoration for ferrets often must begin with habitat restoration and management for prairie dogs.

We focus herein on restoration and management of prairie dogs as a means of restoring ferret populations. First we discuss historical patterns of ferret and prairie dog abundance and, partly on that basis, regional priorities for restoration. Then we describe prairie dog restoration and management methods, challenges to both, and ways of expanding opportunities. Some issues, such as relative habitat quality among the prairie dog species, the influences of plague and predation, and the effects of livestock grazing, also are addressed elsewhere in this volume.

Ferret Habitat: A Historical Perspective

Historical information on ferret habitat is limited because of the fossorial and nocturnal habits of the species (Biggins and Schroeder, 1988) and its early demise. Even so, making the most of available data seems imperative; such data not only provide a rough template for restoration but also can inform the recovery process. The most reliable data primarily include past distributional abundance of ferrets based on verified records (usually collections) and the biogeographical patterns that can be inferred from these records. We recognize that collection records provide a poor surrogate for ferret abundance (numerous factors could influence collection density, as discussed later), but few other historical data sets are as relevant to restoration.

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The general picture that emerges from verified records shows a ferret distributional range largely overlapping the ranges of the three prairie dog species (fig. 1). Black-tailed prairie dog range, being much more extensive than ranges of white-tailed and Gunnison's prairie dogs, encompasses most of the ferret range and accounts for most of the ferret records (Powell, 1982; Anderson and others, 1986). An important question for restoration is whether these records suggest any apparent preferences of ferrets for prairie dog species or biogeographic regions.

If one assumes that density (number per unit area) of ferrets collected or otherwise verified in prairie dog range correlates with habitat quality or preference, Anderson and others' (1986) distribution maps in most cases suggest no clear preference among species within the same regions. Other factors, however, such as proportion of prairie dog range occupied by colonies, could confound judgments of habitat quality based solely on ferret records. Biggins, Lockhart, and Godbey (this volume) and Ernst and others (this volume) note the likelihood that higher density populations of prairie dogs supported more ferrets per unit area, and, as Knowles (2002) indicated, black-tailed prairie dogs usually occur in higher densities than do the other two species. New Mexico presents a conundrum (see also below) in that about four times as many ferret records came from Gunnison's as from black-tailed prairie dog range in the State (Anderson and others, 1986) despite the probable greater density of black-tailed prairie dogs and the estimated similarity in area occupied by the two species (see Hubbard and Schmitt, 1984).

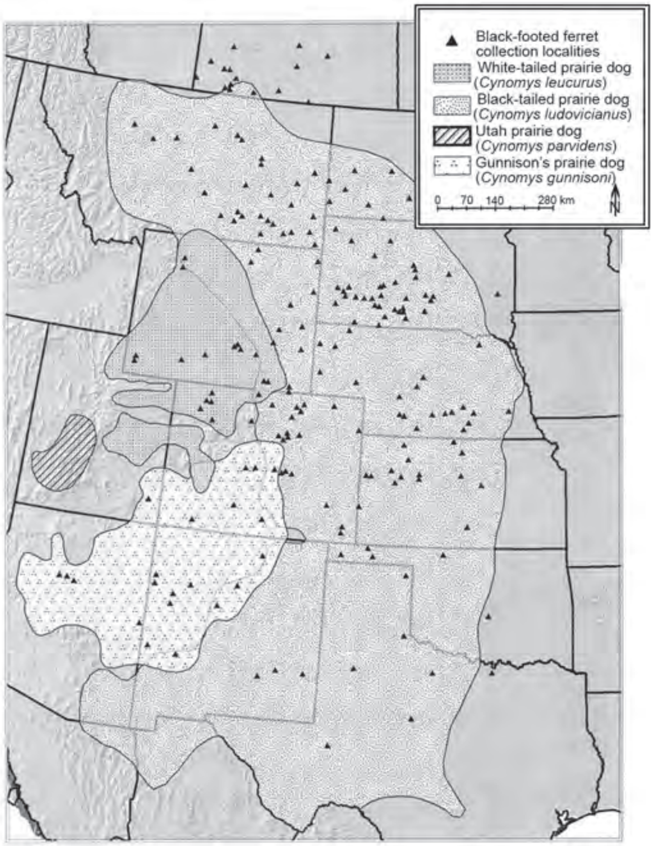

Figure 1. Collection locations for black-footed ferrets (*Mustela nigripes*) (Anderson and others, 1986) and historical ranges of prairie dogs (*Cynomys* spp.) across the Great Plains. Each collection location (dark triangle) represents $\geq$1 verified historical record(s).

The distribution of ferret records in black-tailed prairie dog range suggests that a greater density of ferrets occurred in northern parts than in southern parts. The northern half of the range produced about eight times as many ferret records as did the southern half (calculated from Anderson and others [1986]; fig. 1). Furthermore, numbers of ferret records from Montana, Texas, and the portion of New Mexico occupied by black-tailed prairie dogs (Anderson and others, 1986), viewed in light of estimated prairie dog colony area (table 1), show ferret records per habitat unit in Montana to be about 50 times those in New Mexico and well over 100 times those in Texas. Bailey (1905) described a single colony of black-tailed prairie dogs in Texas that occupied about 65,000 km^2; Anderson and others (1986) showed only two to five ferrets verified from the region occupied by that colony. In comparison, South Dakota's entire prairie dog range (including the unoccupied parts) covered only about twice that area but yielded 99 ferret records. Oklahoma, a southern State with roughly the same area of prairie dog range as that of South Dakota, yielded only four ferret records (Anderson and others, 1986).

Several factors other than habitat quality could have contributed to these north-south differences. Flath and Clark (1986) may have substantially underestimated the area of prairie dog colonies in Montana, and Bailey (1905) may have substantially overestimated it in Texas (D. Gober, oral commun., 2003). Trapping for furs, which accounted for some of the specimens collected (Anderson and others, 1986), may have been more intensive in areas producing better furs—that is, northern regions. The intrusion of agriculture into eastern portions of black-tailed prairie dog range may have occurred earlier in southern than in northern States, perhaps biasing

Table 1. Black-footed ferret (*Mustela nigripes*) collection records from black-tailed prairie dog (*Cynomys ludovicianus*) range in three states, and densities of records within ferret habitat based on reported habitat acreages (i.e., areas occupied by prairie dog colonies).

State	Number of ferret records[a]	Estimated area (km^2) of habitat available	Ferret records/ 100 km^2 of habitat
Montana	44	6,000[b]	0.733
Texas	13	230,000[c]	0.006
New Mexico	3	~21,000[d]	0.014

[a] Anderson and others (1986).
[b] Flath and Clark (1986).
[c] Bailey (1905).
[d] Hubbard and Schmitt (1984).

later collection efforts toward northern States (Anderson and others, 1986). Finally, far southwestern (Chihuahuan Desert) portions of black-tailed range, having historically lacked large wild grazers (Truett, 1996), may have supported low numbers of prairie dogs (and few or no ferrets) prior to the proliferation of cattle (*Bos taurus*) (Hubbard and Schmitt, 1984).

Definitive answers about latitudinal differences in habitat quality of black-tailed prairie dog colonies will come only with comparisons between ferret releases that span the historical range. To date, colony complexes near Janos, Chihuahua, Mexico, host the only ferret releases in southern parts of black-tailed prairie dog range. The youth of this release program precludes a reliable assessment of its success.

Regional Priorities for Restoration

The Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) calls for establishing the widest possible distribution of 10 or more self-sustaining ferret populations. Sites for release of ferrets are selected on the basis of several criteria of habitat suitability (Biggins and others, 1993), key among which are size and expected longevity of prairie dog colony complexes. To complement this strategy, those planning prairie dog restorations probably should set regional priorities. We believe that important criteria for setting such priorities include level of plague risk, species of prairie dog, and regional differences in habitat quality within prairie dog species. All of these criteria will affect relative costs of prairie dog restoration and management.

Plague Risk

The sensitivities of prairie dogs and ferrets to plague make it the most important long-term threat to ferret habitat restoration in regions susceptible to epizootics. The historical spread of sylvatic plague eastward from the west coast and the apparent termination of this advance at the so-called plague line are addressed elsewhere (Cully and Williams, 2001; Gage and Kosoy, this volume). At present, plague apparently occurs in the wild more or less throughout the ranges of white-tailed and Gunnison's prairie dogs and in black-tailed range to about the western borders of South Dakota, Nebraska, Kansas, and Oklahoma—the plague line (Cully and Williams, 2001). The chances of plague epizootics affecting prairie dogs and ferrets west of the plague line seem to vary considerably among localities and to diminish as one nears the line.

Prairie Dog Species

Available evidence suggests to us that, among prairie dog species, the Gunnison's ranks lowest in priority for ferret habitat restoration and that the black-tailed ranks highest. We rank the Gunnison's prairie dog lowest primarily because of the species' relatively high and persisting losses rangewide to plague (Cully and Williams, 2001; Knowles, 2002) and its relatively intact (unaltered) habitat (Knowles, 2002); these factors suggest that restoration and habitat management efforts may lead to little long-term improvement in population status of the species. The average low survival and reproduction of ferrets released into a large Gunnison's prairie dog complex in Arizona (Conservation Breeding Specialist Group, 2004) suggest that, for unclear reasons, ferret habitat quality may be poor (plague appears to be absent at release sites).

We rank the white-tailed prairie dog second in priority. Although also at high risk from plague rangewide, this species is believed to suffer lower losses to epizootics than do Gunnison's or black-tailed prairie dogs, perhaps because of its commonly low population densities (Menkens and Anderson, 1991; Cully and Williams, 2001). In support of this belief, releases of ferrets during 1991–94 into a white-tailed prairie dog complex in Wyoming's Shirley Basin (Luce and others, 1997) resulted in unexpectedly high numbers of ferrets present in 2003 (Grenier, 2003), despite plague epizootics in the interim (Luce and others, 1997; Cully and Williams, 2001). Like Gunnison's prairie dogs, however, white-tails probably offer low per capita returns on investment in restoration and habitat management because of their low density and relatively intact habitat (Knowles, 2002).

We rank the black-tailed prairie dog highest in priority. A substantial proportion of their relatively large range remains plague free, densities within colonies (especially in plague-free areas) tend to be relatively high, and restoration and management efforts can yield high per capita returns. Much of the habitat within their historical range has been degraded, but substantial proportions could be restored. The most successful releases of ferrets have been in plague-free parts of black-tailed prairie dog range (Conservation Breeding Specialist Group, 2004).

Regions Within Black-tailed Prairie Dog Range

Priority for restoration varies from place to place within black-tailed prairie dog range. Most obviously, priority increases with decreased risk of plague. Ferrets released east of the plague line in South Dakota have survived and reproduced much better than those released west of the plague line in Montana (Conservation Breeding Specialist Group, 2004). Also, as noted above, if distributional abundance of ferret records correlates with habitat quality, restoration priority increases with latitude.

Restoration Methods and Challenges

We discuss two aspects of prairie dog restoration: reestablishment of populations and habitat improvement. Hostile traditions toward prairie dogs among land managers represent an important socioeconomic challenge to prairie dog restoration; incentives may help address this challenge.

Translocation

Timely restoration will require reestablishing prairie dogs where they formerly existed. At least three factors will hinder natural recolonization: (1) large spatial vacancies within previously occupied ranges, (2) short dispersal distances of black-tailed prairie dogs (Knowles, 1985) and probably the other species as well, and (3) infrequency with which new colonies originate on their own (Knowles, 1982). Translocations to establish new colonies will greatly accelerate the rate of restoration (D. Long and K. Bly-Honness, unpub. data, 2004).

Unlike natural colonization, translocation can space colonies across landscapes to form complexes ideal for ferrets and compatible with other land uses (see Bevers and others, 1997; Hof and others, 2002). Because small, new colonies expand much faster than large, old ones (Knowles, 1982; D. Long and K. Bly-Honness, unpub. data, 2004), translocation accelerates the rate of population growth. Also, translocation can retard or control unwanted expansion in source colonies by removing substantial proportions of the populations.

Only Utah prairie dogs (*C. parvidens*) and black-tailed prairie dogs have been extensively translocated (Truett and others, 2001a). Translocations of Utah prairie dogs commenced in the early 1970s with concern for the imperiled status of that species. Large-scale translocations of black-tailed prairie dogs have taken place primarily since 1990 (Long and others, in press). Methodologies for both species have been published elsewhere; below we review and compare these methods and recommend approaches that seem to work best for ferret habitat restoration.

Black-tailed Prairie Dogs

Source populations for translocating black-tailed prairie dogs should be selected with attention to disease risks, potential legal restrictions, genetic makeup, and effect of removal on the source population (Truett and others, 2001a; Long and others, in press). To date, plague presents the greatest disease problem and may indicate the need to quarantine animals (Marinari and Williams, 1998) before release. Monkeypox is an emerging disease issue but so far is confined to captive prairie dogs and other rodents. State or Federal restrictions on trapping and transporting prairie dogs may exist; recent restrictions related to monkeypox (U.S. Department of Health and Human Services, 2003) are the most prohibitive to date in that they restrict trapping and transport of all prairie dogs without special exemption. With respect to maintenance of unique gene pools, some biologists have voiced concern about translocating prairie dogs long distances. In practice this concern has influenced few translocation programs, although in New Mexico we acquired prairie dogs from a specific locality to help preserve the gene pool. Using translocations to remove unwanted animals is an attractive idea but in fact is an inefficient and often ineffective control method, in part because most populations seem able to support sustained harvests of at least 25–30 percent annually (T. Livieri, unpub. data, 2002).

The best sites for releases often have evidence of previous occupancy, but risk of plague or encroachment of tall vegetation may have degraded the suitability of such sites (Long and others, in press). Sites without evidence of historical occupancy also can be suitable if soils are deep and relatively fine textured and slopes are less than about 6 percent (Reading and Matchett, 1997). Grass dominance by grazing-resistant species is an important indicator of release site suitability (Long and others, in press).

Operators capture prairie dogs for translocation usually with livetraps but sometimes by pulling them from burrows with a vacuum truck or flushing them out with water (Truett and others, 2001a; Long and others, in press). We advise immediately treating captured animals with a pesticide to kill fleas, which can transmit plague, and then transporting them in wire-mesh cages to quarantine facilities or release sites. Important protocols for handling captive prairie dogs include protection from extreme temperatures, provision of adequate food and water, euthanization if seriously injured, and necropsy of any dying from unknown causes (Marinari and Williams, 1998).

We and most other practitioners conduct translocations during July–September to reduce losses of the very young that would occur with translocations in spring and to give released animals time to excavate new burrows before winter (Long and others, in press). We (Truett and others, 2001a; Long and others, in press) mow tall vegetation at release sites to 10 cm or less and hold the prairie dogs there for several days in acclimation cages consisting of belowground nest boxes connected by an access tube to aboveground retention baskets. The acclimation cages contribute greatly to survival by reducing dispersal and providing shelter from predators during the first few months postrelease while the prairie dogs are excavating new burrows. Predation by coyotes (*Canis latrans*) and badgers (*Taxidea taxus*) during this period usually accounts for most of the postrelease losses; installation of nest boxes at least 1.2 m deep, monitoring for predators at release sites for 2–3 weeks, and selective control of predators during this time commonly result in 50 percent or more surviving onsite at the end of 2 months. By that time, loss rates decline substantially. We usually see recruitment of young at near normal rates the following May and June.

In our experience, most operators translocate prairie dogs in groups as trapped without trying to retain them in original family units or specific sex and age groups. We found no significant difference in postrelease survival or recruitment between groups of prairie dogs translocated as family units ($n = 4$) and those translocated as mixed-family groups ($n = 6$) (Bly-Honness and others, 2004), but Shier (2004) found that five groups she translocated as family units survived and reproduced at higher rates than did five groups trapped without attention to family unity. We found (insignificantly) greater average survival among mixed-family groups translocated after being quarantined together for 2 weeks than among those not quarantined (Bly-Honness and others, 2004). Preliminary data indicated lower survival in groups containing more than about 60 percent juveniles than in groups containing less than about 40 percent juveniles (K. Bly-Honness and D. Long, unpub. data, 2004).

After several months, released animals have usually excavated numerous new secure burrows, and control of depredating coyotes and badgers becomes less important. Occasionally, large losses of prairie dogs at a release site will necessitate supplemental releases during the first several months after the initial release. Supplements usually survive at higher rates than those originally released because they take advantage of the burrows excavated by the first contingent. After several months to a year, management of colonies established by translocation differs little from management of preexisting colonies.

Other Prairie Dog Species

The relatively extensive work on translocation of Utah prairie dogs may instruct efforts to translocate white-tailed and Gunnison's prairie dogs. Utah prairie dogs are more closely related to these two species than are black-tailed prairie dogs, and they occupy similar habitats (i.e., intermountain valleys, benches, and plateaus; Knowles, 2002). Utah prairie dogs were first translocated in 1972, and approximately 20,000 individuals have been moved to date (Long and others, in press). In this section we focus on aspects of these translocations that are different from those discussed above for black-tailed prairie dogs. These differences are rather minor; they include primarily release-site selection and preparation and postrelease protection and monitoring.

Coffeen and Pederson (1993), citing Crocker-Bedford and Spillett (1981), provided criteria for release-site selection for Utah prairie dogs. Sites should be well drained, with soils at least 1.2 m deep and not easily collapsible. Vegetation should be sufficiently short or sparse to allow good horizontal visibility but sufficiently lush to provide forage even in dry periods. Evidence of previous occupancy by prairie dogs increases a site's suitability rating.

Treatment of release sites for Utah prairie dogs has primarily involved removal of tall, dense vegetation and augering of artificial burrows. Player and Urness (1982) demonstrated the benefits of shrub removal to postrelease survival; removal of plants that obstruct horizontal visibility has become standard practice (McDonald, 1993). Augered holes 9–15 cm in diameter and 0.5–1.0 m deep at angles into the ground provide relief from temperature extremes and some level of protection from predators (Player and Urness, 1982; Jacquart and others, 1986; McDonald, 1993). Covering entrances of augered holes with wire-mesh retention baskets to temporarily restrain the prairie dogs and acclimate them to the site (Player and Urness, 1982; Jacquart and others, 1986) appears to improve postrelease survival (McDonald, 1993).

As with black-tailed prairie dogs, mammalian predators, particularly badgers, apparently have caused the greatest losses in translocated Utah prairie dogs (Jacquart and others, 1986; Coffeen and Pederson, 1993; McDonald, 1993). Badger damage has been greatest during the first year or two following release, before the prairie dogs have excavated many secure burrow systems (Jacquart and others, 1986). In comparison, black-tailed prairie dogs usually seem secure from extensive badger depredation after several months (see above). Postrelease monitoring for predators and selective control of badgers are commonly used to protect Utah prairie dogs at release sites (Jacquart and others, 1986; Coffeen and Pederson, 1993). Even so, loss of released animals to badger predation remains a major problem (McDonald, 1993; D. Biggins, written commun., 2003).

Vegetation Management

For several reasons we address primarily black-tailed prairie dogs in this section. This species has a larger historical range that has been proportionately more degraded by agriculture and vegetation change than is the case with white-tailed and Gunnison's prairie dogs (Knowles, 2002). Absence of plague in substantial portions of black-tailed range, coupled with greater average densities of the species, increases the unit-area benefits of habitat restoration. Further, more information exists about habitat restoration and management for black-tailed than for white-tailed or Gunnison's prairie dogs, although the scarcity of information on the latter can be partly offset by the relatively rich database for the Utah prairie dog.

Prairie dogs respond markedly to habitat structure—soil texture, slope, and particularly vegetation height and density (Slobodchikoff and others, 1988; Reading and Matchett, 1997; Truett and others, 2001a). Short vegetation benefits all three species (Longhurst, 1944; Knowles, 1982; Slobodchikoff and others, 1988), presumably because it facilitates visual detection of approaching predators. Black-tailed prairie dogs seem more adversely affected by tall, thick vegetation than do Gunnison's or white-tailed prairie dogs (Scheffer, 1947; Hoogland, 1981; Hubbard and Schmitt, 1984). This effect may be a consequence in part of interspecific differences in predator avoidance behavior (Hoogland, 1981). Detection of predators by visual cues and intraspecific warning calls seem more highly developed in black-tailed prairie dogs, as does clipping of vegetation to improve visibility (Tileston and Lechleitner, 1966; Hoogland, 1996). These characteristics of this species may be evolutionary adaptations to exploit heavily grazed landscapes (Truett, 2003).

Many have noted the positive response of black-tailed prairie dogs to intensive grazing by large herbivores. Osborn and Allan (1949), Snell and Hlavachick (1980), Knowles (1982, 1986), and Cable and Timm (1988) documented expansion of colonies with heavy grazing and their stabilization or shrinkage without grazing in areas supporting mid-height or tall grasses. Truett and others (2001b) and Truett (2003) discussed historical fluctuations in abundance of black-tailed prairie dogs in Great Plains grasslands as a function of changing abundance of large grazers. Other ways of keeping the vegetation short, such as burning or mowing, can substitute for grazing (Ford and others, in press).

Only in shortgrass steppe, which occupies a relatively small part of their historical range (compare fig. 1 with fig. 2), do black-tailed prairie dogs seem relatively free of the need for large grazers (D. Long, unpub. data, 2004). In mixed-grass and tallgrass prairie, sustained absence of grazing (Osborn and Allan, 1949; Knowles, 1982), or simply grazing deferment during the growing season (Snell and Hlavachick, 1980; Snell, 1985), can within a few years or decades exclude black-tailed prairie dogs. This may hold true as well in many historically occupied sites in Chihuahuan Desert grasslands (Truett and Savage, 1998; J. Truett, unpub. data, 2004).

White-tailed, Gunnison's, and Utah prairie dogs tolerate tall, dense vegetation better than do black-tailed prairie dogs. Hoogland (1981) noted the relatively large numbers of shrubs in white-tailed prairie dog colonies (compared with black-tailed colonies) and thought they might serve as protective cover. Taylor and Loftfield (1924) and Longhurst (1944) noted the tolerance of Gunnison's prairie dogs for tall grasses and shrubs in their colonies. Collier and Spillett (1975) and Coffeen and Pederson (1993) indicated that Utah prairie dogs often coexist with, and may benefit from, shrubs.

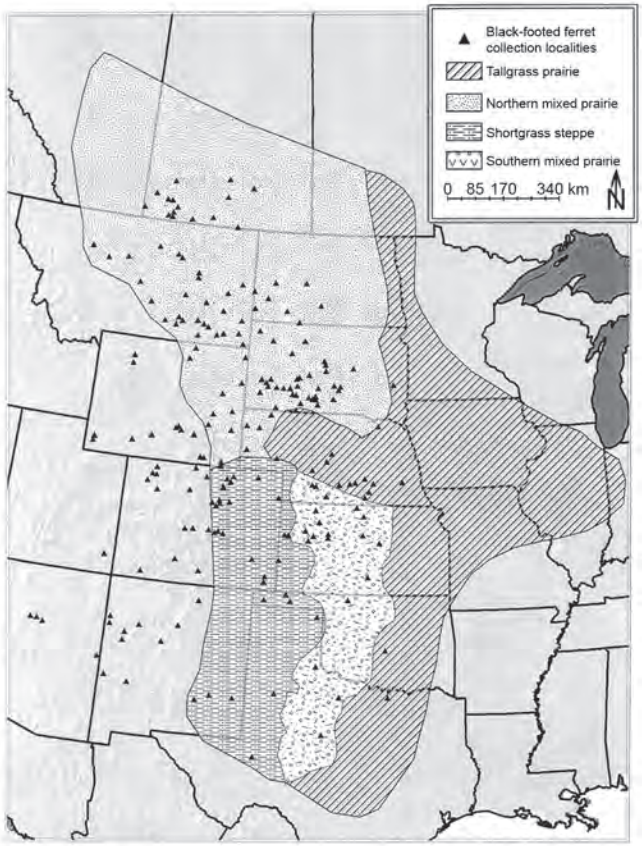

Figure 2. Collection locations for black-footed ferrets (*Mustela nigripes*) (Anderson and others, 1986) and distribution of Great Plains grassland types (Lauenroth and others, 1999). Each collection location (dark triangle) represents ≥1 verified historical record(s).

Still, habitat quality for these species often appears to decline with increasing shrub density beyond some point. Longhurst (1944) described increasing density of Gunnison's prairie dogs with decreasing shrub density and increasing visibility. Collier and Spillett (1975) and the U.S. Fish and Wildlife Service (1991) attributed declines of Utah prairie dogs partly to historical increases in shrub density. As with black-tailed prairie dogs, these species may continue to face declining habitat quality unless tall vegetation (shrubs in this case) can be controlled. The federally threatened status of the Utah prairie dog has prompted attempts at habitat rehabilitation by "chopping" (Coffeen and Pederson, 1993), "roto-beating," "railing," and burning (Player and Urness, 1982) shrubs. Similar efforts to improve habitat for white-tailed and Gunnison's prairie dogs have not been reported.

Socioeconomic Challenges

Aside from plague, the greatest impediment to prairie dog restoration may be hostile traditions among rangeland owners and managers. The historical demise of prairie dogs resulted in large part from control programs aimed at removing a presumed competitor with livestock (Merriam, 1902; Mulhern and Knowles, 1997). Perceptions molded by a century of institutionalized control of prairie dogs (Reading and others, 1999) will be difficult to reverse. To exacerbate the dilemma, livestock production on rangelands has long built on the tradition of moderate grazing uniformly distributed (Fuhlendorf and Engle, 2001), which, especially in mixed-grass and tallgrass prairie, militates against rapid restoration (Truett, 2003).

At a recent symposium on black-tailed prairie dogs, a Colorado rancher was asked why ranchers dislike prairie dogs. In response, he largely dismissed the risk of cattle breaking their legs in burrow entrances but pointed to the loss of forage that could reduce profits. Then, after some hesitation, he offered another important insight—prairie dog colonies simply look bad. Who wants to see his land blighted by the disturbed soil and rodent activity characteristic of prairie dog colonies? In word and gesture he portrayed prairie dogs as symbols of neglect, pariahs of the range, their presence a sign of lax stewardship comparable to an untidy house at Sunday dinner.

Independent of prairie dog control, grazing at light to moderate intensities has come to symbolize good land stewardship among range managers. To many, heavy grazing equates with "overgrazing" and unwise use. This perception took root in the early 1900s with Clements' (1916, 1936) model of "proper" grazing as that which maintained grasslands near climax condition (i.e., dominated by the tallest of the species at a given site). Historical evidence indicates that black-tailed prairie dogs thrived over the moister parts of their original range because of heavy grazing, first by bison (*Bison bison*) and then by cattle (Truett, 2003). Unfortunately for ferret restoration, the relatively moist and plague-free areas in the Great Plains that can support the greatest densities of prairie dogs need the heaviest grazing. Thus, black-tailed prairie dog restoration is squeezed between plague risks from the west and “good” range management from the east.

Managers’ preferences for tall grass compromise another potentially fruitful avenue for prairie dog habitat restoration—reclamation of abandoned farmland (discussed later). The traditional maxim that tall grass is better grass leads most managers to recommend and use seed mixes containing largely tall or mid-height grass species for reclaiming lands such as those under the Conservation Reserve Program (CRP) of the 1985 Food Security Act.

In sum, those in the best position to restore prairie dogs on private and public lands usually lack the motivation to do so. They often come from rural backgrounds, which predisposes them to dislike prairie dogs (Reading and others, 1999). They subscribe to rural traditions that for generations have seen prairie dogs, and the range conditions associated with them, as economically and socially undesirable.

Given the entrenched nature of tradition, must changes in attitude await a new generation of managers with different cultural backgrounds? Perhaps not. For one thing, recent paradigm changes among professionals about what constitutes good conditions on rangelands (discussed later) may legitimize heavy grazing for conservation purposes (Task Group on Unity in Concepts and Terminology, 1995). A more immediate hope builds around incentives, particularly economic ones. Money has a history of reshaping tradition.

Incentives

Landowners, land managers, and agencies that set land management policy potentially can be motivated to restore prairie dogs through at least three kinds of incentives. The most direct and immediately effective incentive is probably economic—money offered to induce change. Regulation or the threat thereof can be brought to bear through the Endangered Species Act (ESA) or other legal means but may generate resentment and thus delay response. Self-motivated cultural change through education is slower still but usually longer lasting. Long-term success in prairie dog restoration may require a combination of all three strategies.

Economic incentives can come from private or public sources, and we can attest to the effectiveness of both. Turner Enterprises, Inc., and the Turner Endangered Species Fund (TESF) have supported prairie dog restoration on private ranches since 1995. Funding from TESF enabled restoration of prairie dog populations on six ranches and also promoted the concept of prairie dog restoration through educational efforts: technical publications, presentations at symposia and meetings, support of university graduate student programs, and field tours to educate people from grade schoolers through governors. Recently TESF funding has been supplemented by matching funds from nongovernment organizations (e.g., National Fish and Wildlife Foundation) and Federal agencies (e.g., U.S. Fish and Wildlife Service Private Stewardship Grants Program, or PSGP). The PSGP awarded grants for prairie dog restoration to other private landowners as well. In 2005, TESF received additional support through the new federally funded State Wildlife Grants Program as matching funds to assist with prairie dog restoration in South Dakota.

The U.S. Fish and Wildlife Service (2000) recently determined that the black-tailed prairie dog was warranted for listing as threatened under the ESA, listing being temporarily precluded by higher priority actions. This finding stimulated the States included in the species’ historical range to collaborate on a conservation strategy (Luce and others, 2001). This strategy has involved a variety of actions including periodic meetings, interagency memoranda of understanding, and agreements on implementation schedules. Fear that management of the species would be assumed by the Federal government motivated this collaboration. The States organized working groups dedicated in part to planning and carrying out restoration actions, and many have completed population estimates and status assessments as a first step toward conservation (Luce and others, 2001). It is too early to assess the extent to which restoration on the ground will result from this action by the Federal government.

Over the longer term, the success of prairie dog and ferret restoration will rely on cultural acceptance of these species as valuable and appropriate components of grassland ecosystems. Private charities, Federal grants, and even government regulations that promote restoration all arose from cultural beliefs that more of nature should be preserved than just the parts generating income. All of these sources of support can disappear without consistent reinforcement of such beliefs. Maintenance of culture-based incentives will require a continuing effort to educate people about the intangible benefits of prairie dogs and other species that have little immediate economic worth. The most enduring incentives are likely to come through intergenerational transmission of values beyond money.

Case Histories

For several years the TESF has been restoring black-tailed prairie dogs on private ranches with the intent of eventually releasing ferrets into the habitat developed. Here we summarize restoration and management efforts on two of these ranches—Vermejo Park Ranch (Vermejo) in shortgrass prairie southwest of Raton, N. Mex., and the Bad River Ranches (Bad River) in mixed-grass prairie west of Pierre, S. Dak. Bison graze both ranches at generally moderate intensities.

Translocations to establish new colonies and protection of prairie dogs from poisoning and shooting have been key to restoration on both ranches. Most releases used source stock from within the respective ranches. Translocation methods followed Long and others (in press). Translocated animals were held for several days prior to release in acclimation cages at the release site; these cages had artificial underground nest chambers that prairie dogs continued to use after release while they excavated new burrows nearby. Predator control focused primarily on coyotes (both ranches) and badgers (Vermejo) during and for a few months following the translocation period. Major field efforts took place during May–October, involving one person on each ranch, with temporary help from another person for 2–3 months during June–August.

Vermejo

Annual monitoring of colony numbers and sizes commenced in 1997. Translocations began in 1999, and from then until 2003 we established 35 new colonies. Two colonies or fewer originated naturally during the 6-year period 1997–2003. Forty-six colonies currently exist, a few formed by the merging of two colonies that were originally separated.

Total area occupied by colonies increased from 202 ha in 1997 to 980 ha in 2003, expanding an average of 31 percent annually (mean of yearly values). Growth rate varied appreciably among colonies, mostly as a function of colony size. Colonies expanded an average of 12 percent per year during 1998–99 when a few large colonies predominated, but expansion increased to an average of 41 percent per year during 2000–03, during which time many small, new colonies were established by translocation.

The short-statured vegetation never seemed to offer much of an impediment to colony growth. Colony growth during 1999, when precipitation and vegetative growth substantially exceeded average, did not differ from that in 1998, when less rain fell. A major drought in 2001 and 2002 (21.8 cm and 23.9 cm, respectively, of precipitation compared with approximately 36.8 cm annual average) greatly reduced vegetative growth and recruitment of young into the prairie dog population but seemed not to influence areal expansion rate of colonies.

Bad River

Annual monitoring of colony numbers and sizes began in 1999, at which time 35 colonies existed. Translocations began in 2000, and from then until 2003 we established 35 new colonies. Eleven new colonies originated naturally during 1999–2003, mostly during a drought year (2002), and six disappeared during a wet year (2001). Seventy-eight colonies, a few having been formed by the merging of two original colonies, existed by late 2003.

Total colony area increased from 271 ha in 1999 to 584 ha in 2003; the average annual increase (mean of yearly values) was 25 percent. Smaller colonies grew faster than larger ones, but the greatest influence on colony growth resulted not from colony size but from grass height and density as a function of precipitation. In 2001, when rainfall and vegetative growth peaked, total colony area shrank 12 percent; in the drought year of 2002 colony area increased 72 percent.

Grazing by bison during years of average or above-average precipitation strongly influenced colony expansion. Heavily grazed colonies in these circumstances expanded at much greater rates than did colonies grazed lightly or not at all. Successful establishment of new colonies in wet years in the absence of grazing required us to mow release sites in summer, sometimes repeatedly, to enhance visibility and postrelease survival. Colonies in an area intensively managed—by establishment of new colonies, grazing at moderate intensities, and mowing as needed—grew 78 percent during the 2-year period that they were managed. Colonies outside this area grew by 29 percent during the same period.

Comparisons and Implications

Colony area in the shortgrass prairie at Vermejo expanded faster on average than that in the mixed-grass prairie at Bad River, and growth rate varied less among years at Vermejo. Our data suggest, however, that the potential average growth at Bad River with intensive grazing or drought may be substantially greater than that at Vermejo. This higher growth rate, coupled with the nearly threefold greater density of prairie dogs at Bad River (D. Long and K. Bly-Honness, unpub. data, 2004), illustrates the great potential that exists for ferret habitat restoration in taller grass regions of the Great Plains. Even so, it may be difficult to maximize this potential without changes in grazing management philosophy, which we discuss below.

Changing Paradigms, New Opportunities

Habitat scarcity seems a looming bottleneck in ferret restoration. The shortage of large prairie dog complexes suitable for ferret release coupled with the increase in ferrets annually available for release suggests a need to evaluate the use of smaller complexes. At the same time, changing philosophies and economics related to the major land uses in ferret range (i.e., grazing and farming) may open new avenues for habitat restoration and management. Below we assess some of the opportunities presented by these changes.

Minimum Size of Prairie Dog Complexes

Clearly, other factors being equal, larger complexes of prairie dog colonies offer better ferret habitat than do smaller ones. Although a high-density colony of black-tailed prairie dogs as small as 10 ha can in theory (Biggins and others, 1993) and in fact (Hillman and others, 1979) support a family of ferrets in the short term, Biggins and others (1993) recommended a minimum 400-ha colony area to sustain a ferret population. The Conservation Breeding Specialist Group

(2004) estimated that 2,440 ha of high-quality habitat (i.e., black-tailed prairie dog colonies in Conata Basin, S. Dak.) would be needed to support 120 breeding adult ferrets with more than 90 percent probability of persistence over 100 years. Moreover, they recommended development of 4,050-ha complexes to achieve ferret recovery objectives.

Given the current scarcity of large complexes secure from poisoning and plague, however, the Conservation Breeding Specialist Group (2004) also recommended investigating ways to enhance ferret recovery by using small (less than 2,000 ha) complexes. Use of smaller sites could attract collaborators (e.g., States and private landowners) excluded by large minimum-area requirements and quickly open up options spanning the entire historical ferret range. Literally and metaphorically, it could plant the seeds needed to ultimately establish larger complexes of prairie dog colonies and the widest possible distribution of ferrets.

Probabilities of extinction rise as ferret population size declines; thus, maintenance of ferrets in small colony complexes might necessitate periodic reintroductions from elsewhere. Still, this inconvenience might be trivial given the possible rewards—attracting wider public and private support, supplying wild-reared kits for release elsewhere, hosting research to better inform a variety of restoration schemes, and maintaining numerous wild populations as a hedge against regional catastrophe. Furthermore, finding ways to use small complexes could ultimately lead to shifts in grazing and farming philosophies to benefit ferret recovery.

New Directions in Grazing: Beyond Clements' Climax

Recently, members of the Task Group on Unity in Concepts and Terminology (1995) of the Society for Range Management laid to rest the conventional notion that grazing according to Clements (1916, 1936) (i.e., maintenance of grass communities near climax) is the sole gospel of good range management. They envisioned an array of potentially "good" grazing management options depending on management goals. In so doing, they legitimized such previously objectionable ideas as intensive grazing in areas of mixed-grass and tallgrass climax to benefit shortgrass species. In our view this change in perspective opened the door conceptually for extending prairie dog and ferret recovery efforts farther eastward into plague-free terrain.

Most ferret records for the Great Plains came from regions where prairie dog populations depended to some extent on grazing; that is, regions dominated by mixed or tall grasses (fig. 2) Historical accounts suggest that grazing by bison, before their demise in the 19th century, facilitated occupancy of these regions by prairie dogs and ferrets; the need for intensive and frequent grazing increased with distance eastward (reviewed by Truett, 2003). Bison had been eliminated in most Great Plains areas well before most ferret collections were made (cf. Anderson and others, 1986; Isenberg, 2000). Prior to bison extirpation, ferrets not only might have been more abundant in eastern portions of their range than numbers collected indicate, but also might have ranged farther east than ecologists have assumed.

Can intensive grazing (by livestock) be reinstated in these eastern, plague-free areas to pave the way for prairie dogs and ferrets? The historical rebound of prairie dogs in some of these areas following entry of cattle in very large numbers in the last decade or two of the 19th century (Merriam, 1902; Truett, 2003) suggests so. Several key management questions surround such a concept.

1. How far east can prairie dogs potentially thrive? Collection records (Hall, 1981) suggest that prairie dogs historically were common farther east than they generally occur now except under anomalous circumstances (e.g., predator-unfriendly sites such as remnant corners of pivot-irrigated fields or human settlements; Sidle and others, 2001; Truett, 2003). Some colonies established by people in high-rainfall areas east of historical range—for example, Nantucket Island off the coast of Massachusetts (Merriam, 1902) and a site east of Fort Worth, Tex. (Schmidly, 1983)—apparently have thrived. In the relatively cool and moist climate of the late Pleistocene, black-tailed prairie dog range extended substantially east of its historical limits (Goodwin, 1995), possibly because of heavy grazing by the numerous megaherbivores of the time (Truett, 2003). The key to prairie dog survival eastward to the limits of historical range and beyond may simply be short grass.

2. What vegetative changes come with the intensive grazing associated with prairie dog occupancy of mixed-grass and tallgrass sites? Mid-height and tallgrass species decline in dominance, often dramatically, and perennial shortgrasses and annuals increase (Detling, 1998; Truett and others, 2001b). Given availability of propagules, shortgrass species such as buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and tumblegrass (*Schedonnardus paniculatus*) increase and often persist in dominance (Archer and others, 1987; Weltzin and others, 1997). Net primary productivity (indicative of forage quantity annually available) typically declines over time, but forage quality increases. Heavy grazing by livestock outside colonies causes similar but usually less dramatic changes (reviewed by Truett and others, 2001b).

3. Would these changes reduce profits from ranching operations? The many variables involved preclude a detailed response, but the short answer is sometimes yes and sometimes no (Detling, 1998; this volume). Prime among the important variables is the proportion

of the landscape occupied by prairie dog colonies. Livestock profits may decline if prairie dog occupancy level is high but may increase if occupancy level is low. For example, Vanderhye (1985) projected substantial benefits to bison at a site in South Dakota where prairie dog colonies occupied only 12 percent of the landscape. Moreover, heavy grazing by cattle to benefit prairie dogs may under some conditions yield greater sustainable profits than would more conventional grazing intensities (Manley and others, 1997; Sims and Gillen, 1999).

Reclaiming Retired Farmland

Large proportions of the plague-free part of the Great Plains have been converted to agriculture; these proportions generally increase with distance eastward and southeastward (Lauenroth and others, 1999). Retirement of farm acreages under programs such as the CRP may offer the potential for prairie dog restoration. Could prairie dogs reoccupy retired farmlands? If so, how should reclamation of such lands proceed?

Black-tailed prairie dogs readily colonize abandoned farmland, often in preference to undisturbed prairie. In Montana, Knowles (1982) found that colonies were disproportionately abundant on previously cultivated lands near abandoned homesteads. In Colorado, Koford (1958) observed that prairie dogs near Fort Collins readily invaded fields under cultivation, and D. Seery (oral commun., 2002) noted that many prairie dog colonies on Rocky Mountain Arsenal National Wildlife Refuge, Colo., occupied long-abandoned fields. In Badlands National Park, S. Dak., Langer (1998) found more and larger prairie dog colonies on long-abandoned farmland than on undisturbed prairie. We observed that prairie dogs near Pierre, S. Dak., quickly invaded land last plowed the previous year.

As expected, cultivated land with tall vegetation repels prairie dogs; land with short or very sparse vegetation attracts them (Koford, 1958). Retired farmland reclaimed with perennial shortgrasses should sustain prairie dogs and, in some circumstances, limit erosion better than if tallgrasses were used in reclamation (see Truett, 2003), the latter a prime goal of the CRP. Mid-height and tall species of grass usually dominate CRP seed mixes (Reynolds and others, 1994; Johnson and Igl, 1995; Patterson and Best, 1996), however, rendering fields reclaimed with such mixes unsuitable for prairie dogs and other shortgrass fauna (e.g., see Kamler and others, 2003). Retired farmlands seem lucrative targets for prairie dog restoration, but seed mixes dominated by shortgrass species would be needed, particularly under programs such as CRP that limit grazing on lands enrolled in the program.

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References Cited

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Archer, S., Garret, M.G., and Detling, J.K., 1987, Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie: Vegetatio, v. 72, p. 159–166.

Bailey, V., 1905, Biological survey of Texas: Washington, D.C., U.S. Bureau of Biological Survey, North American Fauna No. 25, 222 p.

Bevers, M., Hof, J., Uresk, D.W., and Schenbeck, G.L., 1997, Spatial optimization of prairie dog colonies for black-footed ferret recovery: Operations Research, v. 45, p. 495–507.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Biggins, D.E., and Schroeder, M.H., 1988, Historical and present status of the black-footed ferret, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 93–97.

Bly-Honness, K., Truett, J.C., and Long, D.H., 2004, Influence of social bonds on post-release survival of translocated black-tailed prairie dogs (*Cynomys ludovicianus*): Ecological Restoration, v. 22, p. 204–209.

Cable, K.A., and Timm, R.M., 1988, Efficacy of deferred grazing in reducing prairie dog reinfestation rates, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 46–49.

Clements, F.E., 1916, Plant succession: Washington, D.C., Carnegie Institute Publication No. 242, 512 p.

Clements, F.E., 1936, Nature and structure of the climax: Journal of Ecology, v. 24, p. 252–284.

Coffeen, M.P., and Pederson, J.C., 1993, Techniques for the transplant of Utah prairie dogs, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 60–66.

Collier, G.D., and Spillett, J.J., 1975, Factors influencing the distribution of the Utah prairie dog, *Cynomys parvidens* (Sciuridae): Southwestern Naturalist, v. 20, p. 151–158.

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management planning workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

Crocker-Bedford, D.C., and Spillett, J.J., 1981, Habitat relationships of the Utah prairie dog: Logan, Utah, Report prepared by Utah Cooperative Wildlife Research Unit under U.S. Fish and Wildlife Service contract no. 14-16-0008-1117, 29 p.

Cully, J.F., Jr., and Williams, E.S., 2001, Interspecific comparisons of sylvatic plague in prairie dogs: Journal of Mammalogy, v. 82, p. 894–905.

Detling, J.K., 1998, Mammalian herbivores—ecosystem-level effects in two grassland national parks: Wildlife Society Bulletin, v. 26, p. 438–448.

Flath, D.L., and Clark, T.W., 1986, Historic status of black-footed ferret habitat in Montana: Great Basin Naturalist Memoirs No. 8, p. 63–71.

Ford, P.L., Anderson, M.C., Fredrickson, E.L., Truett, J.C., and Roemer, G.W., in press, Effects of fire and mowing on expansion of re-established black-tailed prairie dog colonies in Chihuahuan Desert grassland, *in* Narog, M.G., technical coordinator, Proceedings of the 2002 fire conference on managing fire and fuels in the remaining wildlands and open spaces of the southwestern United States: USDA Forest Service General Technical Report PSW-189.

Fuhlendorf, S.D., and Engle, D.M., 2001, Restoring heterogeneity on rangelands—ecosystem management based on evolutionary grazing patterns: BioScience, v. 51, p. 625–632.

Goodwin, H.T., 1995, Pliocene-Pleistocene biogeography of prairie dogs, genus *Cynomys* (Sciuridae): Journal of Mammalogy, v. 76, p. 100–122.

Grenier, M., 2003, Summary of black-footed ferret activities in Wyoming, 2003: Cheyenne, Wyoming Game and Fish Department, 1 p.

Hall, E., 1981, The mammals of North America: New York, John Wiley and Sons, 2 v., 1,175 p.

Hillman, C.N., Linder, R.L., and Dahlgren, R.B., 1979, Prairie dog distributions in areas inhabited by black-footed ferrets: American Midland Naturalist, v. 102, p. 185–187.

Hof, J., Bevers, M., Uresk, D.W., and Schenbeck, G.L., 2002, Optimizing habitat location for black-tailed prairie dogs in southwestern South Dakota: Ecological Modelling, v. 147, p. 11–21.

Hoogland, J.L., 1981, The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*): Ecology, v. 62, p. 252–272.

Hoogland, J.L., 1996, *Cynomys ludovicianus*: American Society of Mammalogists, Mammalian Species No. 535, p. 1–10.

Hubbard, J., and Schmitt, C., 1984, The black-footed ferret in New Mexico: Sante Fe, New Mexico Department of Game and Fish report to U.S. Bureau of Land Management, 118 p.

Isenberg, A.C., 2000, The destruction of the bison—an environmental history: Cambridge, U.K., Cambridge University Press, 206 p.

Jacquart, H.C., Flinders, J.T., Coffeen, M.P., and Hasenyager, R., 1986, Prescriptive transplanting and monitoring of Utah prairie dog (*Cynomys parvidens*) populations: Salt Lake City, Utah Division of Wildlife Resources, 70 p.

Johnson, D.H., and Igl, D.L., 1995, Contributions of the Conservation Reserve Program to populations of breeding birds in North Dakota: Wilson Bulletin, v. 107, p. 709–718.

Kamler, J.F., Ballard, W.B., Fish, E.B., Lemons, P.R., Mote, K., and Perchellet, C.C., 2003, Habitat use, home ranges, and survival of swift foxes in a fragmented landscape—conservation implications: Journal of Mammalogy, v. 84, p. 989–995.

Knowles, C.J., 1982, Habitat affinity, populations, and control of black-tailed prairie dogs on the Charles M. Russell

National Wildlife Refuge: Missoula, University of Montana, Ph.D. dissertation, 171 p.

Knowles, C.J., 1985, Observations on prairie dog dispersal in Montana: Prairie Naturalist, v. 17, p. 33–40.

Knowles, C.J., 1986, Some relationships of black-tailed prairie dogs to livestock grazing: Great Plains Naturalist, v. 46, p. 198–203.

Knowles, C.J., 2002, Status of white-tailed and Gunnison's prairie dogs: Missoula, Mont., National Wildlife Federation, and Washington, D.C., Environmental Defense, 30 p.

Koford, C.B., 1958, Prairie dogs, whitefaces, and blue grama: Wildlife Monographs, v. 3, p. 1–78.

Langer, T.J., 1998, Black-tailed prairie dogs as indicators of human-caused changes in landscape at Badlands National Park, South Dakota: Raleigh, North Carolina State University, M.S. thesis, 94 p.

Lauenroth, W.K., Burke, I.C., and Gutman, M.P., 1999, The structure and function of ecosystems in the central North American grassland region: Great Plains Research, v. 9, p. 223–259.

Long, D.H., Bly-Honness, K., Truett, J.C., and Seery, D.B., 2006, Establishment of new prairie dog colonies by translocation, *in* Hoogland, J.L., ed., Conservation of the black-tailed prairie dog: Washington, D.C., Island Press, p. 188–209.

Longhurst, W., 1944, Observations on the ecology of the Gunnison prairie dog in Colorado: Journal of Mammalogy, v. 25, p. 24–36.

Luce, B., Gober, P., Van Pelt, B., and Grassel, S., 2001, A multi-state, range-wide approach to black-tailed prairie dog conservation and management: Transactions of the North American Wildlife and Natural Resources Conference, v. 66, p. 464–479.

Luce, B., Oakleaf, B., and Williams, E.S., eds., 1997, Black-footed ferret reintroduction in Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, Annual Completion Report, 1996, 43 p.

Manley, W.A., Hart, R.H., Samuel, M.J., Smith, M.A., Waggoner, J.W., Jr., and Manley, J.T., 1997, Vegetation, cattle, and economic responses to grazing strategies and pressures: Journal of Range Management, v. 50, p. 638–646.

Marinari, P., and Williams, E.S., 1998, Use of prairie dogs in black-footed ferret recovery programs: Laramie, Wyo., U.S. Fish and Wildlife Service, National Black-footed Ferret Conservation Center, 8 p.

McDonald, K.P., 1993, Analysis of the Utah prairie dog recovery program, 1972–1992: Cedar City, Utah Division of Wildlife Resources, 81 p.

Menkens, G.E., Jr., and Anderson, S.H., 1991, Population dynamics of white-tailed prairie dogs during an epizootic of sylvatic plague: Journal of Mammalogy, v. 72, p. 328–331.

Merriam, C.H., 1902, The prairie dog of the Great Plains, *in* Yearbook of the United States Department of Agriculture, 1901: Washington, D.C., Government Printing Office, p. 257–270.

Mulhern, D.W., and Knowles, C.J., 1997, Black-tailed prairie dog status and future conservation planning, *in* Uresk, D.W., Schenbeck, G.L., and O'Rourke, J.T., technical coordinators, Conserving biodiversity on native rangelands—symposium proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-GTR-298, p. 19–29.

Osborn, B., and Allan, P.F., 1949, Vegetation of an abandoned prairie-dog town in tallgrass prairie: Ecology, v. 30, p. 322–332.

Patterson, M.P., and Best, L.B., 1996, Bird abundance and nesting success in Iowa CRP fields—the importance of vegetation structure and composition: American Midland Naturalist, v. 135, p. 153–167.

Player, R., and Urness, P., 1982, Habitat manipulation for reestablishment of Utah prairie dogs in Capitol Reef National Park: Great Basin Naturalist, v. 42, p. 517–523.

Powell, R.A., 1982, Prairie dog coloniality and black-footed ferrets: Ecology, v. 63, p. 1967–1968.

Reading, R.P., and Matchett, R., 1997, Attributes of black-tailed prairie dog colonies in northcentral Montana: Journal of Wildlife Management, v. 61, p. 664–673.

Reading, R.P., Miller, B.J., and Kellert, S.R., 1999, Values and attitudes toward prairie dogs: Anthrozoos, v. 12, p. 43–52.

Reynolds, R.E., Shaffer, T.L., Sauer, J.R., and Peterjohn, B.G., 1994, Conservation Reserve Program—benefit for grassland birds in the northern plains: Transactions of the North American Wildlife and Natural Resources Conference, v. 59, p. 328–336.

Scheffer, T.H., 1947, Ecological comparisons of the plains prairie-dog and the Zuni species: Transactions of the Kansas Academy of Science, v. 49, p. 401–406.

Schmidly, D.J., 1983, Texas mammals east of the Balcones Fault zone: College Station, Texas A&M University Press, 400 p.

Shier, D.M., 2004, Social and ecological influences on the survival skills of black-tailed prairie dogs (*Cynomys ludovicia-*

nus)—a role for behavior in conservation: Davis, University of California, Ph.D. dissertation, 90 p.

Sidle, J.G., Johnson, D.H., and Euliss, B.R., 2001, Estimated areal extent of black-tailed prairie dogs in the northern Great Plains: Journal of Mammalogy, v. 82, p. 928–936.

Sims, P.L., and Gillen, R.L., 1999, Rangeland and steer responses to grazing in the Southern Plains: Journal of Range Management, v. 52, p. 651–660.

Slobodchikoff, C.N., Robinson, A., and Schaack, C., 1988, Habitat use by Gunnison's prairie dogs, *in* Szaro, R.C., Severson, K.E., and Patton, D.R., technical coordinators, Management of amphibians, reptiles, and small mammals in North America: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-166, p. 403–408.

Snell, G.P., 1985, Results of control of prairie dogs: Rangelands, v. 7, p. 30.

Snell, G.P., and Hlavachick, B.D., 1980, Control of prairie dogs—the easy way: Rangelands, v. 2, p. 239–240.

Task Group on Unity in Concepts and Terminology, 1995, New concepts for assessment of rangeland condition: Journal of Range Management, v. 48, p. 271–282.

Taylor, W.P., and Loftfield, J.V.G., 1924, Damage to range grasses by the Zuni prairie dog: Washington, D.C., U.S. Department of Agriculture Bulletin No. 1227, 16 p.

Tileston, J.V., and Lechleitner, R.R., 1966, Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado: American Midland Naturalist, v. 75, p. 292–316.

Truett, J.C., 1996, Bison and elk in the American Southwest—in search of the pristine: Environmental Management, v. 20, p. 195–206.

Truett, J.C., 2003, Migrations of grasslands communities and grazing philosophies in the Great Plains—a review and implications for management: Great Plains Research, v. 13, p. 3–26.

Truett, J.C., Dullum, J.L.D., Matchett, M.R., Owens, E., and Seery, D., 2001a, Translocating prairie dogs—a review: Wildlife Society Bulletin, v. 29, p. 863–872.

Truett, J.C., Phillips, M., Kunkel, K., and Miller, R., 2001b, Managing bison to restore biodiversity: Great Plains Research, v. 11, p. 123–144.

Truett, J.C., and Savage, T., 1998, Reintroducing prairie dogs into desert grasslands: Restoration and Management Notes, v. 16, p. 189–195.

U.S. Department of Health and Human Services, 2003, Control of communicable diseases; restrictions on African rodents, prairie dogs, and certain other animals: Federal Register, v. 68, p. 62353–62369.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

U.S. Fish and Wildlife Service, 1991, Utah prairie dog recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, in cooperation with the Utah Division of Wildlife Resources, 41 p., 6 app.

U.S. Fish and Wildlife Service, 2000, Endangered and threatened wildlife and plants; 12-month finding for a petition to list the black-tailed prairie dog as threatened: Federal Register, v. 65, p. 5476–5488.

Vanderhye, A.V.R., 1985, Interspecific nutritional facilitation—do bison benefit from feeding on prairie dog towns?: Fort Collins, Colorado State University, M.S. thesis, 44 p.

Weltzin, J.F., Dowhower, S.L., and Heitschmidt, R.K., 1997, Prairie dog effects on plant community structure in southern mixed-grass prairie: Southwestern Naturalist, v. 42, p. 251–258.

Black-tailed Prairie Dog Interactions with Other Herbivores: Mediation via Alterations of Vegetation

By James K. Detling[1]

Abstract

Intensive grazing by black-tailed prairie dogs (*Cynomys ludovicianus*) typically reduces graminoid biomass and enhances production and standing crop of less desirable forage species; however, the quality of remaining graminoids is often increased because of higher crude protein concentrations and higher digestibility. Increased forage quality may partially account for why some large grazers such as bison (*Bison bison*), pronghorn (*Antilocapra americana*), and possibly cattle (*Bos taurus*) are attracted to prairie dog colonies as preferred sites to graze. In relatively productive grasslands, grazing and disturbance of tall vegetation by large herbivores apparently allow prairie dogs to expand into areas they might not otherwise occupy. These interactions between prairie dogs and large herbivores do not appear to be as strong in the more arid, less productive shortgrass steppe as in the mixed-grass prairie.

Keywords: bison, cattle, *Cynomys ludovicianus*, forage quality, grazing, plant-animal interactions, pronghorn, trophic interactions

Introduction

At the time that European settlers first migrated westward across North America, prairie dogs (*Cynomys* spp.) occupied vast areas of the Great Plains grasslands. For example, Merriam (1902, p. 258) described a single colony that occupied an area of nearly 65,000 km^2 and contained, by his estimate, 400 million prairie dogs. Much of the area originally inhabited by black-tailed prairie dogs (*C. ludovicianus*) is within the shortgrass and mixed-grass prairies, but they also occupy parts of desert grasslands and shrublands in southern New Mexico and northern Mexico (Hoogland, 1995; Detling, 2006). A large portion of their historical range is now either livestock grazing land or cultivated cropland. Because they can consume or destroy large quantities of forage by clipping, widespread eradication campaigns were mounted during the 20th century to eliminate prairie dogs from much of their original habitat. These campaigns, together with habitat loss and the introduction of bubonic plague into much of their former range, has resulted in an estimated 98 percent reduction in their populations from a century earlier (Miller and others, 1990, 1994). We now know that prairie dogs are important in the maintenance of grassland species diversity and are essential for survival of black-footed ferrets (*Mustela nigripes*) in the wild. Therefore, a number of ecologists and conservation biologists recently have argued for elimination of these eradication campaigns (Miller and others, 1990, 1994; Wuerthner, 1997; Kotliar and others, 1999), which has in turn raised concerns among land managers about how rapidly prairie dog populations might grow, what their effects on grassland vegetation might be, and how this might affect livestock or populations of native grazers.

This paper reviews extant literature pertaining to the above issues with respect to black-tailed prairie dogs. Specifically, I address three questions: (1) How does grazing by prairie dogs affect grassland vegetation? (2) What effects might these changes have on other herbivores? (3) How might grazing by other herbivores affect expansion of prairie dog colonies? Knowing the answers to such questions will enable us to better understand the nature of the habitat used by prairie dogs and associated species such as black-footed ferrets and will assist land managers in assessing some of the consequences of managing for increased area of prairie dog habitat.

Effects of Prairie Dogs on Vegetation

Vegetation Characteristics and Prairie Dog Diets

Most native shortgrass and mixed-grass prairies are dominated by perennial grasses and other graminoids, which may compose as much as 90 percent of the aboveground biomass (Coupland, 1992; Lauenroth and Milchunas, 1992). Although they typically make up a relatively low proportion of the biomass, a diverse group of forbs (i.e., herbaceous dicots) and woody sub-shrubs contribute substantially to overall plant species diversity in most Great Plains grasslands (Sims and others, 1978).

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Prairie dog diets consist largely of native graminoids, and many of the species they consume also compose most of the diets of native and domesticated ungulates (Detling, 2006). For example, on the shortgrass steppe of Colorado (Hansen and Gold, 1977) and the mixed-grass prairie of South Dakota (Uresk, 1984), relatively high-quality forage species such as blue grama (*Bouteloua gracilis*), needleleaf sedge (*Carex eleocharis*), western wheatgrass (*Pascopyrum smithii*), and sand dropseed (*Sporobolus cryptandrus*), all native perennial graminoids, made up about 85 percent of prairie dog diets. In contrast, forbs such as scarlet globemallow (*Sphaeralcea coccinea*) and a sub-shrub, fringed sagewort (*Artemisia frigida*), accounted for the other 15 percent. In addition to consuming vegetation, prairie dogs frequently clip and fell taller vegetation, apparently to enhance predator detection (Hoogland, 1995).

Changes in Plant Cover, Biomass, and Species Composition

As a result of their grazing and clipping behaviors, one of the most striking visual effects that prairie dogs have is a reduction in height of vegetation on their colonies. Where vegetation in uncolonized areas is relatively tall, the visual contrast between colonies and adjacent, uncolonized areas may be substantial. For example, at several mixed-grass prairie sites in South Dakota, vegetation adjacent to prairie dog colonies averaged about 25 cm tall while that on the colonies averaged <10 cm (Archer and others, 1987; Whicker and Detling, 1988a; Russell and Detling, 2003). Another common trend following colonization is a reduction in the amount of standing dead plant biomass relative to live biomass (Coppock and others, 1983a; Detling, 1998). Consequently, prairie dog colonies often appear “greener” than surrounding uncolonized grassland, reminiscent of classical “grazing lawns” (sensu McNaughton, 1984). In drier grasslands with shorter vegetation, such as the shortgrass steppe of eastern Colorado and northern New Mexico, differences in height of vegetation on and off colonies are much less dramatic (Guenther and Detling, 2003), and these colonies may not look greatly different from uncolonized grasslands.

As prairie dog colonies in the northern mixed-grass prairie age following initial colonization of a site, perennial graminoids become weakened by repeated leaf removal and the consequent reduction in their photosynthetic capacity. Not only is shoot biomass of graminoids reduced (Coppock and others, 1983a), but root biomass also declines markedly, particularly in older prairie dog colonies (Ingham and Detling, 1984; Whicker and Detling, 1988b; Detling, 1998). Consequently, over time graminoids lose their competitive dominance and are replaced by forbs and sub-shrubs (Coppock and others, 1983a; Archer and others, 1987). In Badlands National Park, S. Dak., for example, 7 of the 10 most abundant species sampled off prairie dog colonies were graminoids, while 8 or more of the most abundant species on old colonies were forbs (Fahnestock and Detling, 2002). Thus, prairie dog colonies may consist of a variety of vegetation types. Younger parts of colonies are grass dominated and have species composition similar to uncolonized sites but lower biomass and cover. The oldest, most altered parts of colonies are forb dominated and often have little or no graminoid cover or biomass. In addition, as colonies age, the proportion of bare ground tends to increase (Whicker and Detling, 1988b; Russell and Detling, 2003).

Less has been written about vegetation changes following colonization of southern mixed-grass prairie sites. At two >50-year-old colonies in Texas, biomass was only one-third to one-fourth as great on colonies as on uncolonized sites because mid-height grasses had been nearly eliminated (Weltzin and others, 1997a,b). In contrast to northern mixed-grass prairie sites, forb biomass was greater off colonies than on colonies, and biomass of short grasses did not differ significantly on and off colonies.

Available evidence suggests that vegetation is less altered by prairie dogs on the semiarid shortgrass steppe than in mixed-grass prairies. Nevertheless, the general trends appear to be in the same direction as in mixed-grass prairies. For example, in a shortgrass steppe in north-central Colorado, forb cover was greater (5.7 percent) on a colony than off it (3.4 percent), while cover of the dominant grass, blue grama, was lower on the colony (12.2 percent) than off it (19.2 percent) averaged over the growing season (Bonham and Lerwick, 1976). Similarly, Winter and others (2002) reported relatively small differences in vegetation structure and species composition on and off prairie dog colonies in shortgrass steppe in southwestern Kansas and southeastern Colorado. Moreover, bare ground was not significantly greater on colonies than off colonies at the Central Plains Experimental Range in northern Colorado (Guenther and Detling, 2003). These patterns of relatively small effects of prairie dogs on shortgrass steppe vegetation are consistent with the notion that this ecosystem has a long evolutionary history of grazing and is very resistant to heavy grazing (Milchunas and others, 1988), perhaps, in part, a result of the widespread dominance of grazing-resistant blue grama in this grassland type (Lauenroth and Milchunas, 1992).

Changes in Forage Quality

In addition to vegetation changes discussed above, grazing by prairie dogs may alter the phytochemistry and forage quality of plants. One such change involves nitrogen (or crude protein) concentration. In the northern mixed-grass prairie, mean live shoot [N] was 1.3 percent (crude protein = 8.1 percent) in six graminoid species off a prairie dog colony and 1.6 percent (crude protein = 10.0 percent) in the same six species on the colony when averaged over a growing season (Coppock and others, 1983a). Similar trends were observed by Krueger (1986). Moreover, the digestibility of graminoids was greater on prairie dog colonies than on uncolonized areas adjacent to them (Coppock and others, 1983a). Vanderhye's (1985) model results, reviewed by Detling (2006), suggested that changes in forage quality of the magnitude observed on these prairie dog colonies could significantly enhance weight gain of bison (*Bison bison*). Thus, heavy grazing by prairie dogs apparently results in a tradeoff: the quantity of forage species preferred by large grazers declines, but the forage quality of those species is enhanced. Determining the consequences of this quantity-quality tradeoff for cattle (*Bos taurus*) or other large grazers is complicated because the magnitude of the tradeoff likely depends on a variety of factors. These include the type of grassland, length of time a site was inhabited by prairie dogs, past and current management practices, weather conditions, and others. Nevertheless, some simple calculations based on data from a mixed-grass prairie site (Coppock and others, 1983a) might illustrate the approximate magnitude of this tradeoff.

Pringle Valley occupies 120 ha in Wind Cave National Park, S. Dak., and at the time of the study, prairie dogs occupied 36 ha (30 percent) of this valley (table 1). Coppock and others (1983a) recognized three zones within the colony based on length of time colonized: old colony (occupied >26 years), young colony (3–8 years), and edge of colony (<2 years). Since graminoids compose the majority of forage used by livestock, I calculated the effects prairie dogs had on mean growing season biomass, crude protein, and digestible dry matter of graminoids in the valley. These attributes of the forage differed as a function of time colonized (table 1). For example, at the colony edge, mean graminoid biomass per unit area was only 28 percent lower than on adjacent off-colony sites, while on the oldest part of the colony it was 98 percent lower. Because of the higher leaf [N] in plants on colonies (Coppock and others, 1983a), however, the mass of crude protein per unit area was only 12 percent lower at the colony edge (compared to 28 percent lower biomass) than at off-colony sites. Similarly, prairie dog-induced reductions in mass of crude protein in other zones of the colony were not proportionately as great as reductions in graminoid biomass, although they were greater than at the colony edge (table 1). Similar trends occurred for mass of digestible dry matter per unit area, but the magnitude of the compensatory effect was not as great (i.e., reductions in digestible dry matter more closely matched reductions in graminoid biomass) as it was for crude protein (table 1).

The quantity-quality tradeoff also can be illustrated by estimating the total reductions in mean biomass, mass of crude protein, and mass of digestible dry matter attributable to prairie dogs in the entire valley, rather than on a unit area basis (table 1). These estimates were made by multiplying the mass per unit area by the area in each zone of the prairie dog town (table 1) and comparing the totals with the quantity that would have been present if prairie dogs were absent (assuming the same values on the colony as were present in uncolonized grassland). Although the prairie dog colony occupied 30 percent of the area of Pringle Valley, seasonal mean graminoid biomass was only 17.5 percent lower in the valley with prairie dogs present than it would have been with no prairie dogs present, while masses of crude protein and digestible dry matter were 14.6 percent and 16.6 percent lower, respectively. Therefore, had this valley been a paddock on a ranch, available graminoid biomass would have been reduced by prairie dogs proportionately slightly more than available mass of crude protein or digestible dry matter. The difference in the proportional reductions in crude protein and digestible dry matter relative to reductions in biomass represents the approximate magnitude of the quantity-quality tradeoff. Thus, the compensatory effect of prairie dog grazing on forage quality was small compared to their effect on graminoid biomass. It should be stressed, however, that these reductions are greatest on the oldest part of the colony, which suggests that small, relatively young colonies, such as those in areas periodically killed by plague, may have only a small effect on carrying capacity for large grazing animals.

Responses of Other Herbivores to Prairie Dog-Induced Vegetation Changes

Native Herbivores

Some older literature suggests that large native herbivores such as bison and pronghorn (*Antilocapra americana*) may forage preferentially within prairie dog colonies (King, 1955; Koford, 1958). Most of this early literature was based on anecdotal observations and was not well documented with data; however, several subsequent studies have confirmed that such a positive association between large native herbivores and prairie dogs may occur, at least under some conditions.

In northern mixed-grass prairie, Coppock and others (1983b) examined bison use of prairie dog colonies at two different scales in Wind Cave National Park: (1) parkwide use of colonies and (2) use of a single colony in the 120-ha Pringle Valley. The parkwide study involved driving a given route through the entire park three to four times per week from mid-May through mid-October and comparing the proportion of all bison observed that were on colonies to the proportion of landscape occupied by colonies (12 percent). Bison use of prairie dog colonies was greatest during midsummer and, when in the western portion of the park that contained most of the colonies, bison strongly preferred colonies. When their movement patterns took them to the east side of the park (which had fewer colonies), however, bison did not show a preference for prairie dog colonies. Thus, prairie dog colonies did not solely control bison herd movement in the park.

The Pringle Valley study involved mapping, from a nearby fire tower, the location of each bison that entered the valley (Coppock and others, 1983b). When in the valley, bison used the prairie dog colony preferentially over uncolonized portions of the valley. From June through mid-October, they used graminoid-dominated parts of the town two to three

Table 1. Effects of colonization by black-tailed prairie dogs (*Cynomys leucurus*) on seasonal mean mass of graminoids, crude protein in graminoids, and digestible graminoid dry matter in Pringle Valley, Wind Cave National Park, S. Dak. Values were calculated from data on graminoid biomass, nitrogen concentration, and digestibility measured by Coppock and others (1983a) from June 1 to October 1, 1979.

	Off colony	Edge of colony	Young colony	Old colony	Total	% change by prairie dogs
Area occupied (ha)	84	12	15	9	120	-30
Mass per unit area (kg/ha)						
Live graminoids	990	710 (-28%)	410 (-59%)	20 (-98%)	---	
Crude protein	80	71 (-12%)	41 (-49%)	2 (-90%)	---	
Digestible dry matter	499	383 (-23%)	221 (-56%)	11 (-98%)		
Mass in each zone (kg/zone)						
Live graminoids						
Prairie dogs present	83,160	8,520	6,150	180	98,010	-17.5
If prairie dogs were absent	83,160	11,880	14,850	8,910	118,800	
Crude protein						
Prairie dogs present	6,757	852	615	18	8,242	-14.6
If prairie dogs were absent	6,757	965	1,207	724	9,653	
Digestible dry matter						
Prairie dogs present	41,916	4,596	3,315	99	49,926	-16.6
If prairie dogs were absent	41,916	5,988	7,484	4,491	59,879	

times as much as would be predicted by random utilization, and grazing was a predominant activity there. Following a fire in adjacent, uncolonized grassland, bison continued to use the prairie dog colony preferentially but also used the burned area preferentially over the remaining uncolonized, unburned portion of the valley (Coppock and Detling, 1986).

A subsequent study by Krueger (1986) at Wind Cave National Park confirmed and extended this research in several ways. First, in a parkwide study similar to that of Coppock and others (1983b), Krueger (1986) confirmed that bison used prairie dog colonies preferentially. From April through November, about 42 percent of all her bison observations were on prairie dog towns, which covered 12 percent of the sample area. Second, similar to results of Coppock and others (1983b), bison strongly preferred graminoid-dominated parts of colonies (96 percent of all observations) to forb-dwarf shrub-dominated areas (Krueger, 1986). Third, pronghorn also used prairie dog colonies (67 percent of all observations) more frequently than expected from random use (12 percent), and 79 percent of all pronghorn Krueger observed on prairie dog colonies were in areas dominated by forbs and dwarf shrubs. Thus, while bison and pronghorn both used prairie dog colonies preferentially, they made use of different vegetation zones and plant resources within the colonies.

The patterns described above may be modified by precipitation or other weather that affects resources available to grazers. For example, Green (1998) found that bison at Wind Cave National Park used graminoid-dominated parts of prairie dog colonies in proportion to their availability during a year of below average precipitation and forage production; however, in the following year when precipitation and forage production were above normal, bison used these areas preferentially. During the intervening winter, bison avoided prairie dog colonies.

Livestock

Are cattle and other livestock attracted to prairie dog colonies as bison and pronghorn apparently often are? This topic has not been thoroughly researched, so the answer is not clear. On the shortgrass steppe in northern Colorado, cattle used prairie dog colonies approximately in proportion to their availability; that is, they neither preferred nor avoided them (Guenther and Detling, 2003). While on these colonies, however, cattle grazed as intensively as they did in grassland communities not colonized by prairie dogs. Because the shortgrass steppe is quite different from the mixed-grass prairie, it is not possible to say whether the lack of a preference for colonies by cattle was the result of differences in foraging behavior between cattle and bison or differences in large ungulate (e.g., bison and cattle) grazing behavior on shortgrass steppe versus mixed-grass prairie. The result may be more closely related to differences in grassland type, since a year of average precipitation on the shortgrass steppe is similar to a dry year such as that observed by Green (1998) on the mixed-grass prairie.

While this latter idea is somewhat speculative and not supported by data, it is supported by anecdotal observations.

One such observation came in a letter addressed to me and postmarked March 30, 1998, from Mr. Francis Bardanouve, a former long-time member of the House of Representatives in Montana. Mr. Bardanouve was writing in response to statements attributed to me by Long (1998), in which I suggested that bison and pronghorn may graze preferentially on prairie dog colonies because of the higher quality forage there compared to uncolonized areas. Mr. Bardanouve, a self-described lifelong rancher from an area of mixed-grass prairie in northern Montana, wrote:

> I never really [saw] many [prairie dogs] until I began leasing lands on the Ft. Belknap reservation. In a few places it had towns [i.e., colonies] of several hundred acres…[Prairie dogs] cut everything off down to a height of almost less than an inch…There is no grazing left where they are.
>
> However, I have had one mystery which I could never explain. I suddenly realized the answer in your statement. From time to time I would occasionally move cattle within the lease for some reason. What I could never explain was I would be moving them along fine without any trouble until I hit a prairie dog town. It never failed the movement of the bunch [of cattle] would come to a screeching halt. The bunch would begin grazing grass so short you could hardly see it and I could hardly get them moving. I would move one side of the bunch ahead a little and the rest would not move. I would then rush over and shove them ahead and the part that I had just pushed would quit moving. This slow zigzag movement would continue until we were off the "town site" and then the herd would take off at their normal pace.

Clearly, such anecdotal observations should not be taken as scientific evidence that cattle in mixed-grass prairie are attracted to prairie dog colonies as bison or pronghorn are; however, accounts such as these lend some credence to the idea and could perhaps be used as a justification for future studies to address this question.

Does Grazing by Other Herbivores Affect Expansion of Prairie Dog Colonies?

By the early 1900s, settlers and their livestock had moved into much of the Great Plains, and to some it was evident that prairie dog populations were increasing. C. Hart Merriam (1902, p. 263), the former chief of the U.S. Bureau of Biological Survey, noted that "prairie dogs are now more abundant than formerly and their colonies have overspread extensive areas previously unoccupied." He attributed this increase to human-related factors, particularly (1) increasing the food supply for prairie dogs via cultivation of the soil and (2) decreasing the abundance of their natural enemies such as coyotes (*Canis latrans*), badgers (*Taxidea taxus*), hawks, owls, and snakes. Merriam (1902) recognized that prairie dogs caused substantial losses of forage and crops, but he apparently failed to consider that grazing and trampling of vegetation by settlers' livestock might have contributed to the rapid expansion of prairie dog populations.

By the mid-20th century, a number of researchers were beginning to recognize that large grazers might be responsible for expansion of prairie dog colonies. At the Wichita Mountains Wildlife Refuge in southwestern Oklahoma, Osborn and Allan (1949) studied a prairie dog colony that had been designated for complete protection from poisoning. Following termination of all cattle grazing permits in 1937, only native ungulates and a small group of longhorns grazed the 24,000-ha refuge, and very few grazed in the vicinity of this colony. Over the next decade, the study colony completely disappeared. Prairie dogs were known to be a shortgrass plains species and had previously been observed to spread into surrounding vegetation following overgrazing. Therefore, Osborn and Allan (1949) concluded that their initial presence on this site, whose natural climax vegetation was dominated by tall grasses, resulted from heavy grazing during its earlier use as cattle range. Following removal of cattle, they reasoned, grass cover increased in stature and density, and the prairie dogs were restricted to smaller and smaller areas until they eventually died out. By contrast, other colonies at the refuge persisted in spite of at least limited poisoning, but these colonies received regular grazing by bison and other big game (Osborn and Allan, 1949).

The idea that prairie dogs could expand more readily into short vegetation was supported by King's (1955) observations in the mixed-grass prairie of Wind Cave National Park. There, he observed that prairie dogs "invaded" a limestone outcrop covered with short vegetation about 100 m away from the parent colony rather than areas of taller vegetation adjacent to the existing colony. King (1955, p. 105) suggested "that short vegetation may encourage prairie dogs to settle a new area" and that they "seem to select vegetation that is neither too rank nor too tall" as they colonize new areas.

Following his study of prairie dog colonies in northern mixed-grass prairie, shortgrass steppe, and southern mixed-grass prairie, Koford (1958) also noted that prairie dog expansion was favored by shorter, less dense vegetation. In particular, Koford remarked (p. 63) that stands of tall grass surrounding prairie dog colonies could act as effective barriers to expansion, and that prairie dogs "seldom enter grass so tall and thick that they cannot see through or over it." Moreover, he noted (p. 65) that prairie dogs rarely expanded into rangeland that was in good to excellent condition and (p. 67) that "heavy grazing [by livestock] tends to reduce the barriers and allow the spread of prairie dogs." While Koford (1958, p. 67) felt that "conservative grazing" would allow vegetation to grow taller and inhibit prairie dog expansion, he also pointed out that this might not occur in more arid grasslands such as the shortgrass steppe. In support of this idea, Snell and Hlavachick (1980) observed that, after 4 years of rest from livestock grazing during the growing season in southern Kansas, native grasses on a prairie dog colony had become more abundant and the colony had decreased in area from about 45 ha to 5 ha.

Results from more recent studies are consistent with these earlier anecdotal observations and interpretations. For example, in northern mixed-grass prairie in South Dakota, Uresk and Bjugstad (1983) found an average of 106 active prairie dog burrows per hectare on sites where no cattle grazed and more than twice as many (235/ha) where cattle and prairie dogs grazed. They attributed the lower burrow density where cattle were excluded to taller vegetation there and concluded that high prairie dog densities were more likely to occur when rangelands are heavily grazed. In northeastern Montana, Knowles (1986) found that over 60 percent of the colonies he surveyed were on pastures with heavily grazed livestock developments and that nearly all (>97 percent) occurred adjacent to trails and roads. Interviews with landowners and managers suggested to Knowles (1986) that colonization of these areas by prairie dogs followed, rather than preceded, intensive grazing and soil disturbance. Likewise, Licht and Sanchez (1993) suggested that creation of cattle point attractants (e.g., water tanks and supplementary feeding sites) encourages colonization by prairie dogs after vegetation height around the attractants is reduced by livestock grazing and trampling. Similarly, Truett and Savage (1998) noted that expansion of introduced prairie dogs into Chihuahuan Desert grasslands typically only occurred where vegetation was less than 20–25 cm tall. Following mowing of taller vegetation, prairie dogs quickly moved into the mowed areas.

Scholarly reviews of the literature and early accounts of prairie dog interactions with large native and introduced herbivores such as bison and cattle led Truett and others (2001) and Truett (2003) to many of the same conclusions. Specifically, prior to extensive settlement of the Great Plains, the distribution of prairie dogs in more productive grasslands was closely linked to areas frequented by bison, which kept the grass relatively short. Following removal of bison, the range of prairie dogs shrank until cattle were introduced in large numbers, thereby allowing prairie dog populations to expand again. In areas where cattle were introduced soon after extermination of bison, prairie dogs persisted in large numbers; however, severe long-term overgrazing by livestock may reduce densities of prairie dogs by reducing availability of forage resources (Desmond, 2004).

Conclusions

The literature reviewed here suggests a strong interactive relationship between prairie dogs and other grazers, particularly in relatively productive grasslands. We have seen that, as a result of selectively grazing graminoids and clipping the vegetation to a short height, prairie dogs may greatly reduce aboveground plant biomass and cover, change plant species composition towards a greater dominance by forbs, and enhance the quality of the remaining forage via increases in leaf [N] and digestibility. Native grazers, such as bison and pronghorn, as well as cattle, may be attracted to these colonies as preferred sites to graze. Where densities of large grazers are relatively high, their grazing and trampling activities in uncolonized grassland may make some sites more suitable for colonization by prairie dogs and thereby facilitate expansion of prairie dog populations. While much of this latter concept is based on anecdotal reports rather than on experimental results, the preponderance of similar reports (Truett and others, 2001; Truett, 2003) lends credibility to it. In grasslands such as the semiarid shortgrass steppe, where vegetation is naturally shorter and dominated by species such as blue grama, the strength of many of the interactions between prairie dogs and large grazers discussed above is apparently not as strong.

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References Cited

Archer, S., Garrett, M.G., and Detling, J.K., 1987, Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie: Vegetatio, v. 72, p. 159–166.

Bonham, C.D., and Lerwick, A., 1976, Vegetation changes induced by prairie dogs on shortgrass range: Journal of Range Management, v. 29, p. 221–225.

Coppock, D.L., and Detling, J.K., 1986, Alteration of bison and black-tailed prairie dog grazing interaction by prescribed burning: Journal of Wildlife Management, v. 50, p. 452–455.

Coppock, D.L., Detling, J.K., Ellis, J.E., and Dyer, M.I., 1983a, Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity: Oecologia, v. 56, p. 1–9.

Coppock, D.L., Ellis, J.E., Detling, J.K., and Dyer, M.I., 1983b, Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs: Oecologia, v. 56, p. 10–15.

Coupland, R.T., 1992, Mixed prairie, *in* Coupland, R.T., ed., Ecosystems of the world. 8A. Natural grasslands. Introduction and Western Hemisphere: New York, Elsevier, p. 151–182.

Desmond, M., 2004, Effects of grazing practices and fossorial rodents on a winter avian community in Chihuahua, Mexico: Biological Conservation, v. 116, p. 235–242.

Detling, J.K., 1998, Mammalian herbivores: ecosystem-level effects in two grassland national parks: Wildlife Society Bulletin, v. 26, p. 438–448.

Detling, J.K., 2006, Do prairie dogs compete with livestock?, *in* Hoogland, J.L., ed., Conservation of the black-tailed prairie dog: Washington, D.C., Island Press, p. 65–88.

Fahnestock, J.T., and Detling, J.K., 2002, Bison-prairie dog-plant interactions in a North American mixed-grass prairie: Oecologia, v. 132, p. 86–95.

Green, R.A., 1998, Nitrogen distribution in a perennial grassland—the role of American bison: Fort Collins, Colorado State University, Ph.D. dissertation, 126 p.

Guenther, D.A., and Detling, J.K., 2003, Observations of cattle use of prairie dog towns: Journal of Range Management, v. 56, p. 410–417.

Hansen, R.M., and Gold, I.K., 1977, Blacktail prairie dogs, desert cottontails and cattle trophic relations on shortgrass range: Journal of Range Management, v. 30, p. 210–214.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing animal: Chicago, University of Chicago Press, 557 p.

Ingham, R.E., and Detling, J.K., 1984, Plant-herbivore interactions in a North American mixed-grass prairie. III. Soil nematode populations and root biomass on *Cynomys ludovicianus* colonies and adjacent uncolonized areas: Oecologia, v. 63, p. 307–313.

King, J.A., 1955, Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota: Ann Arbor, University of Michigan, Contributions from the Laboratory of Vertebrate Biology No. 67, 123 p.

Knowles, C.J., 1986, Some relationships of black-tailed prairie dogs to livestock grazing: Great Basin Naturalist, v. 46, p. 198–203.

Koford, C.B., 1958, Prairie dogs, whitefaces, and blue grama: Wildlife Monographs, no. 3, 78 p.

Kotliar, N.B., Baker, B.W., Whicker, A.D., and Plumb, G., 1999, A critical review of assumptions about the prairie dog as a keystone species: Environmental Management, v. 24, p. 177–192.

Krueger, K., 1986, Feeding relationships among bison, pronghorn, and prairie dogs—an experimental analysis: Ecology, v. 67, p. 760–770.

Lauenroth, W.K., and Milchunas, D.G., 1992, Short-grass steppe, *in* Coupland, R.T., ed., Ecosystems of the world. 8A. Natural grasslands. Introduction and Western Hemisphere: New York, Elsevier, p. 183–226.

Licht, D.S., and Sanchez, K.D., 1993, Association of black-tailed prairie dog colonies with cattle point attractants in the northern Great Plains: Great Basin Naturalist, v. 53, p. 385–389.

Long, M.E., 1998, The vanishing prairie dog: National Geographic, v. 193, no. 4, p. 116–130.

McNaughton, S.J., 1984, Grazing lawns—animals in herds, plant form, and coevolution: American Naturalist, v. 124, p. 863–886.

Merriam, C.H., 1902, The prairie dog of the Great Plains, *in* Yearbook of the Department of Agriculture (1901): Washington, D.C., U.S. Department of Agriculture, p. 257–270.

Milchunas, D.G., Lauenroth, W.K., and Sala, O.E., 1988, A generalized model of the effects of grazing by large herbivores on grassland community structure: American Naturalist, v. 132, p. 87–106.

Miller, B., Ceballos, G., and Reading, R., 1994, The prairie dog and biotic diversity: Conservation Biology, v. 8, p. 677–681.

Miller, B., Wemmer, C., Biggins, D., and Reading, R., 1990, A proposal to conserve black-footed ferrets and the prairie dog ecosystem: Environmental Management, v. 14, p. 763–769.

Osborn, B., and Allan, P.F., 1949, Vegetation of an abandoned prairie-dog town in tall grass prairie: Ecology, v. 30, p. 322–332.

Russell, R.E., and Detling, J.K., 2003, Grasshoppers (Orthoptera: Acrididae) and black-tailed prairie dogs (*Sciuridae: Cynomys ludovicianus* (Ord))—associations between two rangeland herbivores: Journal of the Kansas Entomological Society, v. 76, p. 578–587.

Sims, P.L., Singh, J.S., and Lauenroth, W.K., 1978, The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics: Journal of Ecology, v. 66, p. 251–285.

Snell, G.P., and Hlavachick, B.D., 1980, Control of prairie dogs—the easy way: Rangelands, v. 2, p. 239–240.

Truett, J.C., 2003, Migrations of grassland communities and grazing philosophies in the Great Plains—a review and implications for management: Great Plains Research, v. 13, p. 3–26.

Truett, J.C., Phillips, M., and Miller, R., 2001, Managing bison to restore biodiversity: Great Plains Research, v. 11, p. 123–144.

Truett, J.C., and Savage, T., 1998, Reintroducing prairie dogs into desert grasslands: Restoration and Management Notes, v. 16, p. 189–195.

Uresk, D.W., 1984, Black-tailed prairie dog food habits and forage relationships in western South Dakota: Journal of Range Management, v. 37, p. 325–329.

Uresk, D.W., and Bjugstad, A.J., 1983, Prairie dogs as ecosystem regulators on the northern high plains, *in* Kucera, C.L., ed., Proceedings of the Seventh North American Prairie Conference, August 4–6, 1980: Columbia, University of Missouri, Division of Biological Sciences, p. 91–92.

Vanderhye, A.V.R., 1985, Interspecific nutritional facilitation—do bison benefit from feeding on prairie dog towns?: Fort Collins, Colorado State University, M.S. thesis, 44 p.

Weltzin, J.F., Archer, S., and Heitschmidt, R.K., 1997a, Small-mammal regulation of vegetation structure in a temperate savanna: Ecology, v. 78, p. 751–763.

Weltzin, J.F., Dowhower, S.L., and Heitschmidt, R.K., 1997b, Prairie dog effects on plant community structure in southern mixed-grass prairie: Southwestern Naturalist, v. 42, p. 251–258.

Whicker, A.D., and Detling, J.K., 1988a, Ecological consequences of prairie dog disturbances: BioScience, v. 38, p. 778–785.

Whicker, A.D., and Detling, J.K., 1988b, Modification of vegetation structure and ecosystem processes by North American grassland mammals, *in* Werger, M.J.A, van der Aart, P.J.M., During, H.J., and Verhoeven, J.T.A., eds., Plant form and vegetation structure—adaptation, plasticity and relation to herbivory: The Hague, The Netherlands, SPB Academic Publishing, p. 301–316.

Winter, S.L., Cully, J.F., Jr., and Pontius, J.S., 2002, Vegetation of prairie dog colonies and non-colonized shortgrass prairie: Journal of Range Management, v. 55, p. 502–508.

Wuerthner, G., 1997, Viewpoint—the black-tailed prairie dog—headed for extinction?: Journal of Range Management, v. 50, p. 459–466.

Shooting Prairie Dogs

By Archie F. Reeve[1,2] and Timothy C. Vosburgh[3]

Abstract

Recreational shooting of prairie dogs (*Cynomys* spp.) has occurred for many years, but interest and intensity have increased dramatically in the past decade. Shooting can cause prairie dogs to change their behavior and can affect sex and age groups differently. Prairie dog populations are capable of recovering from shooting or other reductions, but time to full recovery depends on demographic parameters (survivorship and fecundity). Simple population growth models with demographic variability demonstrate less risk of population extinction when shooting is regulated by effort rather than by quotas on numbers shot. Landowners might consider allowing shooting as a source of income, but, if not closely managed, shooters potentially can eliminate small colonies. Predation by black-footed ferrets (*Mustela nigripes*) probably does not significantly depress prairie dog populations. Prairie dog mortality caused by unregulated recreational shooting can vastly exceed predation by black-footed ferrets, affecting prairie dog survivorship and potentially affecting fecundity and recruitment. Until effects of shooting prairie dogs as prey for black-footed ferrets are better understood, shooting closures on reintroduction sites are appropriate.

Keywords: black-footed ferret, *Cynomys* spp., *Mustela nigripes*, prairie dog, recreational shooting

Introduction

Many long-time residents of western States recall spending summer vacations “plinking” prairie dogs (*Cynomys* spp.), whether by wrist rocket, air gun, or .22 caliber rifle. For over 100 years, shooting black-tailed prairie dogs (*C. ludovicianus*) in rural Kansas, for example, was common on Sunday afternoons by self-styled “varmint hunters” and by after-school target shooters (Smith, 1967). Shooting prairie dogs has been and continues to be primarily for sport but now involves marksmen who utilize high-technology rifles while practicing their shooting skills. To hone their skills, many shooters use a variety of rifles, scopes, range finders, shooting benches, and reloading equipment. Indeed, shooting prairie dogs at distances >450 m entitles one to membership in the 500 Yard Club, sponsored by the Varmint Hunters Association, and some members have registered successful shots >1,350 m.

Many shooters come from out of State (Vosburgh, 2000; South Dakota Prairie Dog Work Group, 2001), but this appears to be a recent phenomenon. In North Dakota, for example, nonresidents must purchase either a nongame license or a combination nongame and furbearer license to shoot prairie dogs; residents are exempt (North Dakota Game and Fish Department, 2001). The number of nonresident nongame licenses sold increased from 36 in 1975 to 625 in 2001, while nonresident nongame and furbearer license sales increased from 163 in 1989 to 1,326 in 2001 (S. Hagen, written commun., 2003). The recent increase in license sales to nonresidents in North Dakota indicates the rise in recreational shooting of prairie dogs by people from out of State. Similarly, in South Dakota over 35 percent of the estimated 16,011 prairie dog shooters on nontribal land in 2001 were nonresidents (Gigliotti, 2001).

Shooting Intensity

Available information indicates that substantial numbers of prairie dogs have been shot. In 2000, recreational shooters killed 1,186,272 prairie dogs on nontribal lands in South Dakota (South Dakota Prairie Dog Work Group, 2001). The number killed on nontribal lands increased to 1,516,174 in 2001 (Gigliotti, 2001). Shooters spent a total of 75,059 recreation days to kill that many prairie dogs: 54,849 by residents and 20,210 by nonresidents (Gigliotti, 2001).

During 1998 in Nebraska, 7,100 shooters spent 33,400 recreation days killing 301,000 prairie dogs; in 1999, fewer shooters (5,970) spent less time (28,300 recreation days) to kill more prairie dogs (356,000) (Nebraska Game and Parks Commission, 2001). The Colorado Division of Wildlife (2002) estimated (with ±95 percent confidence interval) that 6,070 shooters (±629) killed 418,412 prairie dogs (±75,234) during 64,674 recreation days (±825) in the 1998–99 reporting period. Based on these data, shooter success rates (number killed per recreation day) appear similar among reporting States: 6.5 killed per day in Colorado (between 5.2 and 7.7), 12.6 killed per day in Nebraska in 1999, and 20.3 killed per day in South Dakota in 2001.

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Estimates of prairie dogs killed in individual States depend on shooters' responses to survey questionnaires, which are possible only when shooters are licensed, such as in South Dakota and Colorado (South Dakota Prairie Dog Work Group, 2001; Colorado Division of Wildlife, 2002, 2003). On the other hand, nontribal recreational shooters on some tribal lands are required to be accompanied by a guide and must fill out a questionnaire that includes the number of days spent shooting, number of rounds fired, and estimated number of prairie dogs killed. In 2000, 936 shooters fired 156,307 rounds to kill 57,848 prairie dogs on the Rosebud Indian Reservation (T. Vosburgh, unpub. data, 2002). That rate of one prairie dog killed per 2.7 rounds fired is similar to an observed rate of one prairie dog killed per 3.0 shots fired on the Fort Belknap Indian Reservation in northern Montana during 2001 (Vosburgh, 2000).

The Lower Brule Indian Reservation in central South Dakota has collected 9 years of black-tailed prairie dog harvest data (table 1). From 1993 to 2001, an average of 121 licensed recreational shooters killed an average of 14,200 prairie dogs per year while spending an average of 372 recreation days on the reservation (Lower Brule Sioux Tribe, 2002). Each shooter averaged 118 prairie dogs shot per year or about 38 shot per day. That level of success is comparable to nonresident shooters on nontribal lands in South Dakota who, in 2001, spent an average of 3.5 days per shooter to kill 36 prairie dogs per day (Gigliotti, 2001). The average success rate was higher than reported above by Nebraska or Colorado. Relatively high levels of shooter success may be due to tribes' interest in recreational shooting as a source of revenue with concomitant monitoring of shooting effects on prairie dog populations. Also, out-of-State shooters may be especially diligent in pursuit of their quarry. During 2001, residents of South Dakota shot an average of 14 prairie dogs per day, considerably fewer than the 36 prairie dogs per day reported shot by nonresidents (Gigliotti, 2001).

Shooter success rates appear related to prairie dog densities. Typical densities of black-tailed prairie dogs exceed those of white-tailed prairie dogs (*C. leucurus*) (Tileston and Lechleitner, 1966), whereas densities of Gunnison's prairie dogs (*C. gunnisoni*) are intermediate or overlap those of the other two species (Fitzgerald and others, 1994). All three species are shot in Colorado, but harvest estimates are not reported by species, only by county (Colorado Division of Wildlife, 2003). Based on species' distributions (Fitzgerald and others, 1994), we estimated harvest for the three species (table 2). Although ranges of shooting success rates overlap, shooters in 2002–03 killed more prairie dogs per recreation day in counties with black-tailed prairie dogs than in counties inhabited by Gunnison's and/or white-tailed prairie dogs (table 2).

Effects of Shooting on Individual Prairie Dogs

Prairie dogs subjected to shooting change their behavior. In Montana, black-tailed prairie dogs in colonies with recreational shooting spent less time above ground than did prairie dogs in colonies with no shooting. When above ground, the former devoted less time to feeding and more time to scanning than the latter (Vosburgh and Irby, 1998). Prairie dogs in colonies with recreational shooting are more likely to escape when approached on foot or by vehicle, retreating to burrows sooner than prairie dogs not subjected to shooting (Vosburgh and Irby, 1998; Keffer and others, 2000). Increased alertness and early escape by prairie dogs are potential problems for recreational shooters, though some shooters may by more interested in shooting skill and firearm accuracy than in numbers of prairie dogs killed.

The timing of shooting prairie dogs may affect reproduction and mortality of various sex and age groups. Shooting from March to May is likely to kill pregnant or lactating females so that neither they nor their offspring will reproduce the following year (Knowles, 1988). Shooters generally cannot distinguish between male and female prairie dogs and, except during early summer, between adults and juveniles. Juvenile prairie dogs are more susceptible than adults to low levels

Table 1. Data from 9 years of shooting black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation, S. Dak.[a]

	Year								
Statistic	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**
Number of licenses sold	115	146	139	127	157	97	114	130	64
Estimated total killed	17,700	28,000	4,600	10,700	15,300	16,700	12,100	14,800	8,069
Total recreation days	367	503	334	486	372	392	363	319	211
Harvest/day/shooter	48	56	14	22	41	43	33	46	38
Average days/shooter	3.2	3.6	2.4	3.8	2.8	2.9	3.2	2.5	3.3

[a] Lower Brule Sioux Tribe (2002).

Table 2. Harvest estimates for three species of prairie dogs (*Cynomys*)—white-tailed (*C. leucurus*), Gunnison's (*C. gunnisoni*), and black-tailed (*C. ludovicianus*)—in Colorado during 2002–03 with rates and ranges of number killed per recreation day.

Species[a]	Number of counties in distribution[a]	Number of hunters[b]	Recreation days spent[b]	Total prairie dogs killed[b]	Shooter kill rate (number/day)	Range (number/day) for counties
White-tailed	5	1,063	13,197	30,943	2.34	0.78–5.51
White-tailed with Gunnison's	2	394	12,153	66,772	5.49	4.76−5.71
Gunnison's	12	827	9,278	31,533	3.40	0.00−6.44
Gunnison's with black-tailed	3	197	1,083	3,762	3.47	3.25−3.65
Black-tailed	20	1,948	17,845	170,867	9.58	1.42−101

[a] Counties within species' distributions as described by Fitzgerald and others (1994).

[b] Colorado Division of Wildlife (2003).

of shooting (Keffer and others, 2000). For example, when a colony having 35 percent juveniles was subjected to a 10 percent harvest during early to mid-summer, 53 percent of the animals killed were juveniles. On the same colony, adult females and adult males (39 percent and 26 percent of the population, respectively) were killed proportionately less than their occurrence in the population. Higher shooting pressure (>20 percent mortality) on another colony also targeted juveniles disproportionately (Keffer and others, 2000).

Adult females, including yearlings, appear more vulnerable to shooting than do adult and yearling males (Vosburgh and Irby, 1998; Keffer and others, 2000). During early summer 1995 in Montana, for example, the ratio of adult males to females was 92:100 on nine colonies (Vosburgh and Irby, 1998). In late summer, after an average of 8.5 hours of shooting per colony, the ratio of adult males to adult females was 167:100 on the same nine colonies. Survivorship of adult females during shooting was only 57 percent of the survivorship of adult males. On eight control colonies with no shooting, adult female survivorship was 122 percent of adult male survivorship between early and late summer in the same year (Vosburgh and Irby, 1998), which is similar to differential survival of unhunted black-tailed prairie dog populations elsewhere (Hoogland, 1995). Greater vulnerability of females probably exacerbates the impact of shooting by diminishing future reproduction.

Reproduction by adult and yearling female prairie dogs may be suppressed on colonies that are subject to continual recreational shooting. In North Dakota, only 32 percent of yearling female black-tailed prairie dogs on colonies disturbed by >20 years of heavy shooting reproduced (based on placental scars and evidence of ovulation) compared with 90 percent of yearling females on colonies relatively undisturbed by shooting (Stockrahm and Seabloom, 1988). Counts of placental scars in adult females ($\geq$2 years old) examined from the disturbed colonies were significantly lower than in adult females on relatively undisturbed colonies, indicating depressed reproduction on the disturbed colonies. These observations do not demonstrate that continual shooting was solely responsible for depressed reproduction because the disturbed colonies were spatially confined and not growing, whereas the undisturbed colonies were not spatially restricted and had doubled in size during the previous 5 years (Stockrahm and Seabloom, 1988). Depressed reproduction in the disturbed though confined colonies, especially by yearling females, may indicate density-dependent processes similar to those observed by Garrett and others (1982) in South Dakota.

Effects of Shooting on Prairie Dog Populations

Populations increase with birth and immigration of individuals but decrease with their death or emigration. For species such as prairie dogs that reproduce once a year (Hoogland, 1995) but die from various sources throughout the year, information about the rate of population increase (sometimes called the "finite rate of increase" and symbolized here by R; others often use lambda, λ) is important to understanding potential effects of recreational shooting on colonies. The equation $N_t = N_0 R^t$ can be used to compute population size at time t, N_t, if the initial population size, N_0, and R are known.

Finite rates of increase in prairie dog colonies with no shooting vary from year to year. For example, at one black-tailed prairie dog colony in Wind Cave National Park, S. Dak., colony size increased in some years but declined in others. Population finite rates of increase at this colony averaged 1.03 (1 standard deviation = 0.25), with minimum R = 0.70 and maximum R = 1.45 (Hoogland, 1995, table 16.1). Because this colony was surrounded by unsuitable habitat, its area remained constant, so the observed R = 1.0 might have been expected. Stationary populations often increase in response to factors such as addition of food, increase in habitable area, and population reduction (Caughley and Sinclair, 1994). Population reduction decreases competition, usually for food. With more food per individual, reproduction increases, mortality decreases, and the population grows (Caughley and Sinclair, 1994).

Limited experimental evidence demonstrates that removing prairie dogs, by shooting or other means, enhances population growth rates. After 2 consecutive years of shooting at two small black-tailed prairie dog colonies, populations were reduced or eliminated; in the year after shooting ceased, portions of both colonies were still inactive (Knowles, 1988). Five years after the shooting program ended, the larger of the two shot colonies had expanded to cover 140 percent of its preshooting area, and the smaller had grown to cover 90 percent of its former area (Knowles, 1988). Spatial growth of these treatment colonies resulted from increased numbers of prairie dogs, but details of population increase—whether by immigration from neighboring colonies or as a demographic response of the surviving prairie dogs—are unavailable. Data on active versus inactive burrow entrances indicate a similar response to cessation of shooting at larger black-tailed prairie dog colonies in South Dakota. Less than 45 percent of total burrows were active while recreational shooting was allowed, but, after 4 years without shooting, 74 percent of burrow entrances were active (B. Perry, unpub. data, 2000).

Rates of population increase have been documented under other conditions that reduce prairie dog populations. Knowles (1986) studied the effects of a toxicant, zinc phosphide, on several black-tailed prairie dog colonies by different treatment regimes and then observed the population recoveries for up to 5 years following the treatments. Knowles computed instantaneous growth rates for each year during population recovery. The instantaneous growth rate, r, is related to the finite rate of increase, R, by $R = e^r$, (Akçakaya and others, 1999) and is employed to predict population growth in continuous time rather than in discrete time, by the equation $N_t = N_0 e^{rt}$. One month after treatments that attempted to completely eradicate two colonies, Knowles (1986) estimated a reduction of 95 percent caused by the treatments. By continuing to monitor population recovery, Knowles computed average r = 0.916 (R = 2.499) after 1 year, r = 1.069 (R = 2.912) from the first to the second year and r = 0.350 (R = 1.419) from the second to the fifth year. For the five colonies that received partial toxicant treatment, which reduced target populations to an average of 19 percent of pretreatment levels, average r = 1.339 (R = 3.815) after 1 year and r = 0.148 (R = 1.160) from the first to the second year (Knowles, 1986).

Values for R reported by Knowles (1986) were higher for both study groups after the first year following treatments than values observed on a prairie dog colony in Wind Cave National Park, S. Dak. That colony expanded from 0.47 ha to 1.86 ha over a 3-year period (Garrett and Franklin, 1988) when colony size in June increased from 51 to 134 adults and juveniles (average R = 1.38). Similarly, a black-tailed prairie dog colony near Nunn, Colo., with no population reduction treatment, expanded from 2.1 ha to 3 ha in 1 year as the colony size in June grew from 28 to 82 animals (Koford, 1958, p. 10, table 1). For that colony in that 1-year period, R = 2.93, but in the previous year the colony had declined from 50 to 28 animals (R = 0.56).

Population responses were also tracked following reduction of two colonies in South Dakota by translocating live-trapped black-tailed prairie dogs (Radcliffe, 1992). After intensive removal during June of the first study year, 6 prairie dogs remained in one of the colonies, but 10 were present by June of the following year. By June of the second year following removal, the population had increased to 51 prairie dogs, but the increase was mostly attributed to immigration (Radcliffe, 1992). The second colony also grew substantially after the population was reduced to 10 individuals in June of the treatment year. By the next June that colony had grown to 23 and by June of the second year had grown to 80 prairie dogs; the extraordinary growth rate during the second year was R = 3.48. In this second colony, immigration played a minor role (three immigrated annually). Population growth mainly resulted from increased litter size and higher juvenile survivorship (Radcliffe, 1992).

These data support our earlier generalization that populations can be stimulated to grow by reducing the number of animals that compete for a limited resource. Similar population responses were noted in colonies of Gunnison’s prairie dog during and after a sylvatic plague epizootic in Moreno Valley, N. Mex. Cully (1997) found that after plague killed more than 99 percent of the population, the few surviving prairie dogs formed two colonies in areas that were previously unoccupied. Using Leslie matrix analysis involving demographic parameters (survivorship and fecundity), Cully found that the population would be nearly tripling each year. The key to this high rate of population growth was found to be yearling females reproducing at a rate similar to that of adults and having a relatively high survival rate (Cully, 1997). Similarly, the survival rate of juveniles (90 percent) in a young, expanding black-tailed prairie dog colony in South Dakota was significantly higher than juvenile survivorship (49 percent) in an older, nonexpanding colony (Garrett and others, 1982). In addition, yearling females on the younger colony were more likely to produce and wean a litter than were those on the older colony. These two demographic characteristics of juveniles and yearlings appear consistent in rapidly growing prairie dog populations.

Simulated Effects of Different Shooting Strategies

In many of these studies, prairie dog populations appear to exhibit density-dependent growth; crowding with concomitant diminishing resources available to each individual leads to increased mortality (decreased survival), decreased reproduction, and/or increased emigration. An assumption of density-dependent population growth is that when a population approaches carrying capacity (K) the growth rate declines and eventually reaches R = 1.0 when N = K. The value of R at time t, R_t, depends on the population size N_t relative to K according to the equation, $R_t = R_{max}^{(1-Nt/K)}$. When the population N_t is small, the exponent $(1 - N_t/K)$ is close to 1 and the population's growth rate R_t is close to the maximum possible, or R_{max}. As the population grows and approaches its carrying capacity, the growth rate R is much less than R_{max}, and when the population reaches carrying capacity, R = 1.0 because the exponent $(1 - N_t/K) = 0$.

If prairie dogs are viewed as an economic resource, the best strategy is to manage colonies for a sustained yield. A landowner or wildlife manager hoping to capitalize on prairie dog harvest might allow shooters to kill as many prairie dogs in a year as are produced. With density-dependent growth ($R_{max} = 2.00$, K = 1,000), a population growing from 20 to 1,000 animals produces the maximum number of animals (maximum yield) when it is approximately at half of carrying capacity (Peek, 1986). In this example, maximum yield = 209 when the population reaches 438 after 5 years of growth.

Harvesting the population at maximum productivity maximizes yield, but managing for maximum yield is difficult (Caughley and Sinclair, 1994). Removing animals from a population reduces the base population. The difficult task is determining what base population produces the best yield for the next year. If the harvest exceeds maximum yield and continues over time, the population will eventually decline to zero (Caughley and Sinclair, 1994).

Two common approaches to control harvest are (a) imposing a quota on numbers harvested and (b) regulating harvesting effort (Caughley and Sinclair, 1994). Regulating harvest by quotas is conceptually attractive: once the quota is attained, shooting stops. Determining when quotas for prairie dogs are reached might be problematic, however. If shooters consistently record prairie dogs killed and number of rounds fired, wildlife managers can estimate the number killed from the number of shots. Figure 1 demonstrates the problem with fixed annual harvest quotas. An initial population of 1,000 eventually stabilizes at 585 animals in 24 years if 195 prairie dogs are shot each year, but if the annual harvest exceeds 209 animals (the maximum yield when $R_{max} = 2.00$ and K = 1,000), then the population declines to extinction, doing so faster with larger harvests.

Theoretically, controlling harvest effort removes some proportion of the population over time rather than a fixed number of animals each year. One way to control harvest effort is to limit the timing and duration of the harvest. Another way is to limit the number of shooters (Caughley and Sinclair, 1994). Figure 2 shows the outcome of various annual harvest levels as percentages of the current population. At an annual harvest rate of 25 percent, the population stabilizes at 585 animals, but in only 13 years, while the long-term average harvest (from t = 0 to t = 30) is approximately 199 animals.

To this point, population growth was assumed to be deterministic with no uncertainty in birth or death rates. Environmental variation from year to year, or day to day, and from one locale to another causes fluctuations in prairie dog populations' birth and death rates (Hoogland, 1995). In addition, individual animals in the same population have different reproductive capabilities or chances of survival. Recreational shooting of prairie dogs introduces additional uncertainty in

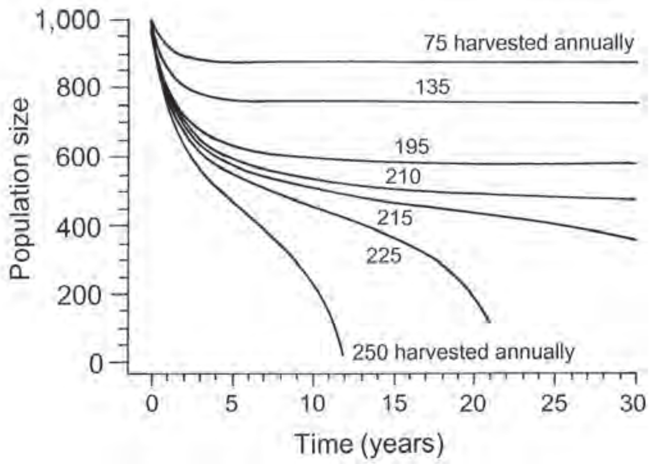

Figure 1. Effects of constant annual harvest quotas on a population with density-dependent growth ($R_{max} = 2.00$, K = 1,000) but no random variation in R_t. Annual harvest >209 animals (maximum yield) cannot be sustained, and the population eventually declines to zero.

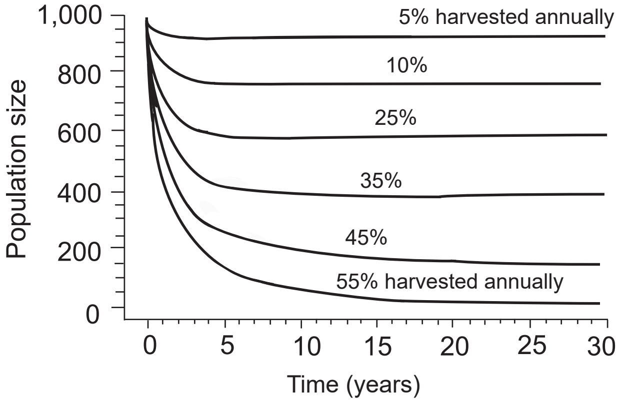

Figure 2. Deterministic predictions of a population with density-dependent growth ($R_{max} = 2.00$, K = 1,000) subject to different levels of proportional harvest annually.

population demographic parameters since age groups and sexes may be affected differently. Levels of variability might be measured at some point in time but cannot be predicted in the future. Stochastic population models provide for such uncertainty.

In the simulation examples provided so far, the finite rate of increase at time t, R_t, is equal to $R_{max}^{(1-Nt/K)}$. Annual variation in rates of birth, immigration, death, and emigration all contribute to variability of R_t. Annual variation in carrying capacity also causes variation in R_t. We introduce variation by increasing or decreasing the computed value of R_t by a random amount but within some defined limits, for example within ±20 percent of the computed value for R_t, which includes demographic variation as well as random variation in carrying capacity.

This simple approach was applied in 100 simulations to project population growth from an initial population of 20 animals with R_{max} = 2.0 and K = 1,000. The simulations show that the average population size stabilizes at approximately 1,000 animals (fig. 3) but, because of random variability of R_t, the population at t = 15 could range from 797 to 1,230 animals in any one simulation.

Random variation, now limited to only ±15 percent of the computed value for R_t, for example, is used to predict how an initial population of 1,000 (N_0 = K) with R_{max} = 2.0 responds to an annual quota of 195 animals harvested. The results (fig. 4) are different from those generated by the deterministic model (fig. 1). After 1,000 simulations, the stochastic model predicts a population of 406 (ranging from 0 to 819) at the end of 30 years with average annual harvest of 183. The model also predicts a 23 percent chance that the population will become extinct by t = 30. Risk of extinction increases with level of random variation in R_t. For example, with random variation ±10 percent of R_t, extinction within 30 years occurred in 1 percent of the trials, but a 46 percent chance of extinction is expected with random variation ±20 percent of R_t (after 1,000 simulations with an annual quota of 195).

Alternatively, an annual harvest rate of 25 percent produces an expected population of 580 animals (ranging from 439 to 744 animals) after 30 years of simulation with average annual harvest of 197 animals but poses no risk of extinction (fig. 5), unlike the risk observed with fixed quota harvest (fig. 4). With demographic and environmental uncertainty, sustainable populations are more likely if harvested proportionally rather than by fixed quota. Implicit in modeling these two harvest strategies, however, is intensity of harvest management. Once set, the quota of 195 harvested did not change over time even though the population may have been declining

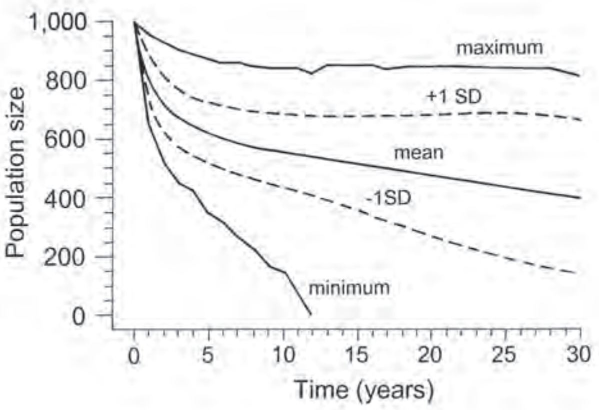

Figure 4. Results of 1,000 simulations with an annual harvest quota of 195 animals, an initial population of 1,000 animals, density-dependent population growth (R_{max} = 2.00), and random variation in the population growth rate each year (within ±15% of R_t after computation as $R_t = R_{max}^{(1-Nt/K)}$).

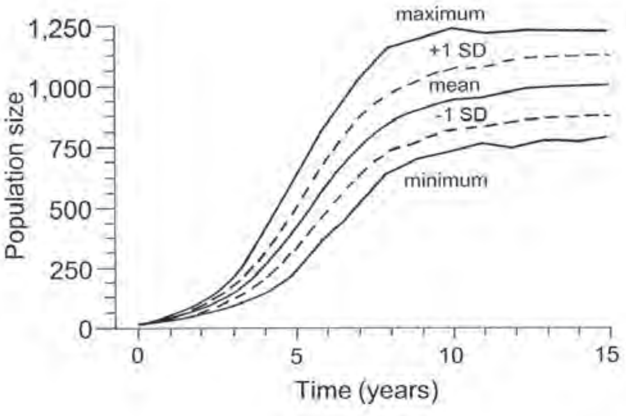

Figure 3. Results of 100 simulations of density-dependent population growth (R_{max} = 2.00, K = 1,000), but with random variation in the population growth rate each year (within ± 20% of R_t after computation as $R_t = R_{max}^{(1-Nt/K)}$).

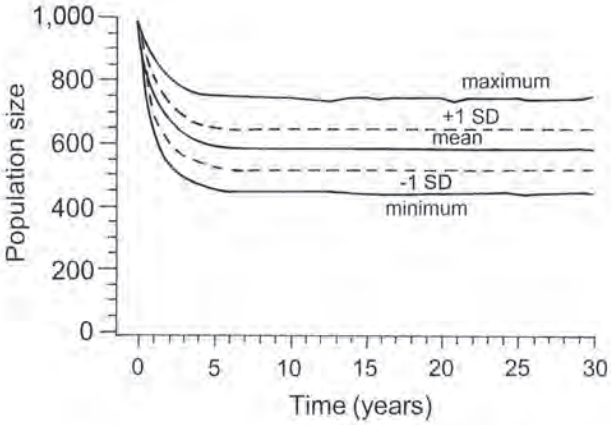

Figure 5. Results of 1,000 simulations with an annual harvest rate of 25%, an initial population of 1,000 animals, density-dependent population growth with R_{max} = 2.00, and random variation in the population growth rate each year (within ±15% of R_t after computation as $R_t = R_{max}^{(1-Nt/K)}$).

in a given simulation. Alternatively, numbers harvested were continuously adjusted when a harvest rate of 25 percent was applied. To ensure a sustainable population while realizing a desired annual harvest, the manager must monitor the dynamics of the target population and respond accordingly.

Proper application of either harvest strategy, whether by regulating harvest quota or by regulating harvesting effort, requires knowledge of the target population's carrying capacity and the species' R_{max}. Seldom are these parameters known with any certainty. A population at approximately K/2 is expected to yield the maximum number of animals that, in theory, could be harvested each year as a maximum sustained yield (MSY). Nevertheless, stochastic events in the environment and variability among individuals in a population can lead to substantial population fluctuations, and harvest should always be well below the estimated MSY (Caughley and Sinclair, 1994).

A third approach involves harvesting only when a population exceeds some threshold level, above which excess animals are taken (Lande and others, 1997). Threshold harvesting requires specific knowledge about population levels but produces high annual variation in harvest because populations below the threshold are not harvested (Lande and others, 1997). Threshold harvesting might be possible if a manager or landowner had never attempted to control prairie dogs and had monitored population levels under various environmental conditions so that average K could be estimated.

Recreational Shooting on Private Land for Prairie Dog Conservation

Of >660 livestock and agricultural operators surveyed in eastern Wyoming (Wyoming Agricultural Statistics Service, 2001), 23 percent expressed interest in a program of financial compensation for allowing prairie dogs on their land. The survey posed four types of management programs to respondents who expressed interest in financial compensation: (a) a shooting management program, (b) a cooperative shooter placement program to direct shooters to landowners willing to allow shooting, (c) a program to develop markets for prairie dogs as pets or for nature photography, and (d) a banking program in which other States would compensate Wyoming landowners for conserving prairie dogs (Wyoming Agricultural Statistics Service, 2001). Of these, prairie dog banking was the most popular (59 percent interested), a cooperative shooter placement program (57 percent interested) was second, followed by interest in shooting management (51 percent of respondents).

Respondents who expressed interest in programs with financial compensation considered \$74−\$86/ha annually to be reasonable (\$30−\$35/acre, median value). Generally, interest in maintaining or increasing the number of acres of prairie dog colonies on their land varied directly with the level of financial compensation. To attain \$74−\$86/ha in potential income from shooting, a landowner with 405 ha (1,000 acres) of prairie dog colonies, for example, could charge four shooters \$79−\$92 per person per day to shoot during the period between Memorial Day and Labor Day (approximately 95 days). Four shooters during that period are equivalent to 380 recreation days. Applying data from the Fort Belknap Indian Reservation (average of 38 prairie dogs shot per recreation day), the annual toll would be 14,440 prairie dogs killed, whereas 2,470 killed would be expected in a year at the rate of 6.5 prairie dogs per recreation day estimated in Colorado.

Densities of black-tailed prairie dogs in Conata Basin, S. Dak., range from 8/ha to 41/ha (Severson and Plumb, 1998). If that range of densities is applied to the simple example of a 405-ha colony on private land, then the population, estimated between 3,240 and 16,605 prairie dogs, could eventually be eliminated by recreational shooting under either the shooter success rate on Fort Belknap Indian Reservation or in Colorado. To ensure a future income, the private landowner would have to significantly decrease the number of recreation days spent shooting, which should concomitantly decrease the number of prairie dogs shot. In addition, to attain the desired income, the landowner would have to substantially increase fees charged per shooter.

Managing prairie dogs on private land for recreational shooting might be appropriate for some landowners and not others. Still, when faced with the apparent need or desire to control prairie dogs, opening land to shooters can provide landowners with an additional source of income and thus an incentive to support some level of occupied habitat that they otherwise would not tolerate.

Recreational Shooting on Black-footed Ferret Reintroduction Sites

Recreational shooting of prairie dogs has been totally or partially restricted on black-footed ferret (*Mustela nigripes*) reintroduction sites (Colorado Division of Wildlife and others, 2002), although there are few instances where effects of shooting closures on prairie dog populations have been monitored. In some instances, shooting closures coincided with changes in statewide prairie dog management practices following States' adoption of the Black-tailed Prairie Dog Conservation Assessment and Strategy and addendum (Luce, 2001). Closures to shooting have also been applied to other species of prairie dog, as in Arizona where black-footed ferrets were introduced in Gunnison's prairie dog colonies (B. Van Pelt, oral commun., 2003). In other cases, shooting closures were initiated to improve habitat for introduced black-footed ferrets and to ensure that ferrets, especially kits, would not be inadvertently shot (B. Perry, oral commun., 2003). Other wildlife, burrowing owls (*Athene cunicularia*) in particular, can be killed during recreational shooting of prairie dogs. Though not documented as a consequence of shooting prairie dogs, there are instances of substantial burrowing owl mortality by shooting (Haug and others, 1993; James and Espie, 1997).

In its review of a petition to list the black-tailed prairie dog under the Endangered Species Act, the U.S. Fish and Wildlife Service (1999) evaluated effects of recreational shooting, concluding in part that shooting may be a compensatory source of mortality in large populations with substantial reproduction. Where small prairie dog populations are depressed by other factors such as disease, shooting may be an additive source of mortality. Compensatory mortality, where one source of mortality offsets or replaces another source (Mackie and others, 1990), whether caused by harvest or predation, is most likely to occur in populations near their ecological equilibrium or carrying capacity (Peek, 1986; Bartmann and others, 1992; Boyce, 2000). In such density-dependent regulated populations, when density is high so are mortality rates, and a population decrease by whatever means results in higher survivorship in the remaining population, as long as removal of animals does not adversely affect reproduction the following year. When removal by harvest and/or predation is high enough to affect reproduction in subsequent years, mortality from those sources is likely to be additive and, if extreme, can force the target population to extinction.

By most accounts, ferret predation does not significantly depress prairie dog populations (Fagerstone, 1987) and would seem a source of compensatory mortality. Biggins and others (1993) estimated annual consumption of 109 prairie dogs by one black-footed ferret family group (1 adult female, 3.3 young, and 0.5 adult male) while recognizing the potential for substantial prairie dog predation by other species. Assuming moderate levels of mortality by other sources, Biggins and others (1993) estimated that a stable population of 763 prairie dogs would sustain a ferret family group for 1 year. Using an age-dependent predation model of ferrets and prairie dogs, Klebanoff and others (1991) concluded that as many as 2,000 prairie dogs per ferret may be necessary to sustain a stable predator-prey system. A stable system can also be attained with fewer prairie dogs—though not as few as 763—but only if prairie dog survivorship or fecundity rates increase (Klebanoff and others, 1991). We are not aware if either estimation approach has been field tested.

Prairie dog mortality by unregulated recreational shooters can vastly exceed predation by black-footed ferrets, thus affecting prairie dog survivorship and potentially affecting fecundity and recruitment. Recreational shooting can be additive mortality, potentially more so on black-tailed prairie dog colonies than on Gunnison's or white-tailed colonies (table 2). Management agencies have recognized that, even with closures of specific areas, recreational shooting has continued and that enforcement of shooting closures is problematic (V. Kopcso, oral commun., 2003). Until more is known about effects of recreational shooting on prairie dogs that are the primary prey resource for black-footed ferrets, managers are wise to restrict shooting and enforce closures, particularly on ferret reintroduction sites inhabited by black-tailed prairie dogs.

References Cited

Akçakaya, H.R., Burgman, M.A., and Ginzburg, L.R., 1999, Applied population ecology principles and computer exercises using RAMAS® EcoLab 2.0: Sunderland, Mass., Sinauer Associates, Inc., 285 p.

Bartmann, R.M., White, G.C., and Carpenter, L.H., 1992, Compensatory mortality in a Colorado mule deer population: Wildlife Monographs, v. 121, p. 1–39.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Boyce, M.S., 2000, Modeling predator-prey dynamics, *in* Boitani, L., and Fuller, T.K., eds., Research techniques in animal ecology—controversies and consequences: New York, Columbia University Press, p. 253–287.

Caughley, G., and Sinclair, A.R.E., 1994, Wildlife ecology and management: Cambridge, Mass., Blackwell Science, 334 p.

Colorado Division of Wildlife, 2002, 1998/99 small game harvest survey statistics: http://wildlife.state.co.us/hunt/small_game/89_99smgamesurveystats1.htm.

Colorado Division of Wildlife, 2003, 2002/03 small game harvest report: http://wildlife.state.co.us/hunt/small_game/harvest_statistics_02-03/small_game_harvest.pdf.

Colorado Division of Wildlife, Bureau of Land Management, and U.S. Fish and Wildlife Service, 2002, Prairie dog shooting and black-footed ferret recovery in northwest Colorado: Grand Junction, Colo., U.S. Fish and Wildlife Service, 13 p.

Cully, J.R., Jr., 1997, Growth and life-history changes in Gunnison's prairie dogs after a plague epizootic: Journal of Mammalogy, v. 78, p. 146–157.

Fagerstone, K.A., 1987, Black-footed ferret, long-tailed weasel, short-tailed weasel, and least weasel, *in* Novak, M., Baker, J.A., Obbard, M.E., and Malock, B., eds., Wild furbearer management and conservation in North America: Ontario, Canada, Ministry of Natural Resources, p. 548–573.

Fitzgerald, J.P., Meaney, C.A., and Armstrong, D.M., 1994, Mammals of Colorado: Niwot, Denver Museum of Natural History and University Press of Colorado, 467 p.

Garrett, M.G., and Franklin, W.L., 1988, Behavioral ecology of dispersal in the black-tailed prairie dog: Journal of Mammalogy, v. 69, p. 236–250.

Garrett, M.G., Hoogland, J.L., and Franklin, W.L., 1982, Demographic differences between an old and a new colony of black-tailed prairie dogs (*Cynomys ludovicianus*): American Midland Naturalist, v. 108, p. 51–59.

Gigliotti, L., 2001, Prairie dog shooting in South Dakota: Pierre, South Dakota Department of Game, Fish and Parks, 35 p.

Haug, E.A., Millsap, B.A., and Matell, M.S., 1993, Burrowing owl (*Speotyto cunicularia*), *in* Poole, A., and Gill, F., eds., The birds of North America: Washington, D.C., American Ornithologists' Union, and Philadelphia, Pa., Academy of Natural Sciences, no. 61, p. 1–20.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing mammal: Chicago, University of Chicago Press, 557 p.

James, P.C., and Espie, R.H.M., 1997, Current status of the burrowing owl in North America—an agency survey, *in* Liner, J.L., and Steenhof, K., eds., The burrowing owl, its biology and management—including the Proceedings of the First International Symposium: Raptor Research Report, no. 9, p. 3–5.

Keffer, K., Gordon, K., and Anderson, S., 2000, Effects of recreational shooting on behavior of black-tailed prairie dogs: Laramie, University of Wyoming, Cooperative Fish and Wildlife Research Unit, 15 p.

Klebanoff, A., Minta, S., Hastings, A., and Clark, T.W., 1991, Age-dependent predation model of black-footed ferrets and prairie dogs: SIAM Journal of Applied Mathematics, v. 51, p. 1053–1073.

Knowles, C.J., 1986, Population recovery of black-tailed prairie dogs following control with zinc phosphide: Journal of Range Management, v. 39, p. 249–251.

Knowles, C.J., 1988, An evaluation of shooting and habitat alteration for control of black-tailed prairie dogs, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: Fort Collins, Colo., USDA Forest Service, General Technical Report RM-154, p. 53–56.

Koford, C.B., 1958, Prairie dogs, whitefaces, and blue grama: Wildlife Monographs, v. 3, p. 1–78.

Lande, R., Saether, B., and Engen, S., 1997, Threshold harvesting for sustainability of fluctuating resources: Ecology, v. 78, p. 1341–1350.

Lower Brule Sioux Tribe, 2002, Black-tailed prairie dog management plan: Lower Brule, S. Dak., Lower Brule Sioux Department of Wildlife, Fish, and Recreation, 18 p.

Luce, B., ed., 2001, Addendum—an umbrella, multi-state approach for the conservation and management of the black-tailed prairie dog, *Cynomys ludovicianus*, in the United States: Cheyenne, Wyo., Black-tailed Prairie Dog Conservation Team, 22 p.

Mackie, R.J., Hamlin, K.L., Pac, D.F., Dusek, G.L., and Wood, A.K., 1990, Compensation in free-ranging deer populations: Transactions of the North American Wildlife and Natural Resources Conference, v. 55, p. 518–526.

Nebraska Game and Parks Commission, 2001, Nebraska conservation plan for the black-tailed prairie dog: Lincoln, Nebraska Game and Parks Commission, draft report, July 2001, http://www.ngpc.state.ne.us/wildlife/pdogplan.html.

North Dakota Game and Fish Department, 2001, Black-tailed prairie dog state management plan: Bismarck, North Dakota Game and Fish Department, 14 p.

Peek, J.M., 1986, A review of wildlife management: Englewood Cliffs, N.J., Prentice-Hall, 486 p.

Radcliffe, M.C., 1992, Repopulation of black-tailed prairie dog (*Cynomys ludovicianus*) colonies after artificial reduction: Frostburg, Md., Frostburg State University, M.S. thesis, 30 p.

Severson, K.E., and Plumb, G.E., 1998, Comparison of methods to estimate population densities of black-tailed prairie dogs: Wildlife Society Bulletin, v. 26, p. 859–866.

Smith, R.E., 1967, Natural history of the prairie dog in Kansas: Lawrence, University of Kansas, Museum of Natural History and State Biological Survey of Kansas, 39 p.

South Dakota Prairie Dog Work Group, 2001, South Dakota black-tailed prairie dog management plan: Pierre, South Dakota Department of Game, Fish and Parks, draft report 2—October 2001, 74 p., http://www.sdgf.info/Publications/pdmplan.pdf.

Stockrahm, D.M.B., and Seabloom, R.W., 1988, Comparative reproductive performance of black-tailed prairie dog populations in North Dakota: Journal of Mammalogy, v. 69, p. 160–164.

Tileston, J.V., and Lechleitner, R.R., 1966, Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado: American Midland Naturalist, v. 75, p. 292–316.

U.S. Fish and Wildlife Service, 1999, Positive 90-day finding for a petition to list the black-tailed prairie dog: Denver, Colo., U.S. Fish and Wildlife Service, Region 6, 50 p.

Vosburgh, T., 2000, Impacts of recreational shooting on prairie dogs on Fort Belknap Reservation, Montana, *in* Vosburgh, T., and Stoneberg, R., eds., 1999 annual report of black-footed ferret recovery activities: Fort Belknap Reservation, Mont., 4 p.

Vosburgh, T.C., and Irby, L.R., 1998, Effects of recreational shooting on prairie dog colonies: Journal of Wildlife Management, v. 62, p. 363–372.

Wyoming Agricultural Statistics Service, 2001, Black-tailed prairie dog management survey, report of results: Cheyenne, Wyoming Department of Agriculture, 21 p.

Habitat Preferences and Intraspecific Competition in Black-footed Ferrets

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Abstract

We used radio-telemetry data (28,560 positional fixes) collected on 153 black-footed ferrets (*Mustela nigripes*) to (1) reexamine the assumed obligate relationship of these ferrets to prairie dogs (*Cynomys* spp.), (2) investigate habitat preferences of ferrets at a small scale (<1 ha), and (3) gain insight into competition among ferrets for habitat patches of varying quality. We used densities of prairie dog burrows as an indicator of habitat quality because burrows are presumably valuable to ferrets as cover and because density of burrows is correlated to density of prairie dogs. Burrow density summaries were generated from maps of all burrows on ferret reintroduction sites in Montana and South Dakota. Aboveground movements by ferrets were mostly (89 percent) within the boundaries of prairie dog colonies or associated with circuits involving return to a colony (10 percent), with no evidence that ferrets sought to occupy alternative habitats. Sampling with 0.07-ha plots suggested that dispersion of prairie dog burrows within colonies was neither uniform nor random. Burrows were clumped, and ferrets preferred ($P < 0.001$) patches of habitat with high densities of burrows compared to samples taken at random points on the colonies they occupied. The magnitude of preference (the difference between use and availability) was greatest for resident young ferrets compared to their recently released counterparts, whether the newcomers were compared with residents of 2–4 weeks ($P = 0.039$) or >1 year ($P = 0.048$). Also, preference was stronger for wild-born young ferrets than for young captive-born ferrets released to augment the wild population ($P = 0.040$). This additional evidence for competition among ferrets, and for an advantage of prior residency, raises conservation concerns. The energetics-based model commonly used to predict ferret densities at reintroduction sites does not consider competition, which likely leads to overestimation of the densities of ferrets attainable in high-quality habitat. During sequential releases of ferrets, prior residency may handicap success of newcomers, even though the latter may have higher potential fitness. Although the manner of initial colonization of available habitat by black-footed ferrets, and their subsequent competition for it, was suggestive of an ideal despotic distribution, we did not assess effects of prey density or burrow density on fitness.

Keywords: black-footed ferret, competition, *Cynomys*, endangered species, habitat, ideal despotic distribution, ideal free distribution, *Mustela nigripes*, prairie dog, prior residency

Introduction

Conservation efforts for the highly endangered black-footed ferret (*Mustela nigripes*) include a captive breeding program that rescued the species from a remnant population of 10 animals in Wyoming (fig. 1) during the winter of 1985–86. That captive breeding program currently produces annual surpluses of 200–300 kits for reintroduction (Marinari and Kreeger, this volume). Ferrets have been reintroduced at sites in six U.S. States and Chihuahua, Mexico (Lockhart and others, this volume). Releases of ferrets into unoccupied and occupied habitat, and monitoring of wild-born ferrets, provided unique opportunities to evaluate large-scale habitat

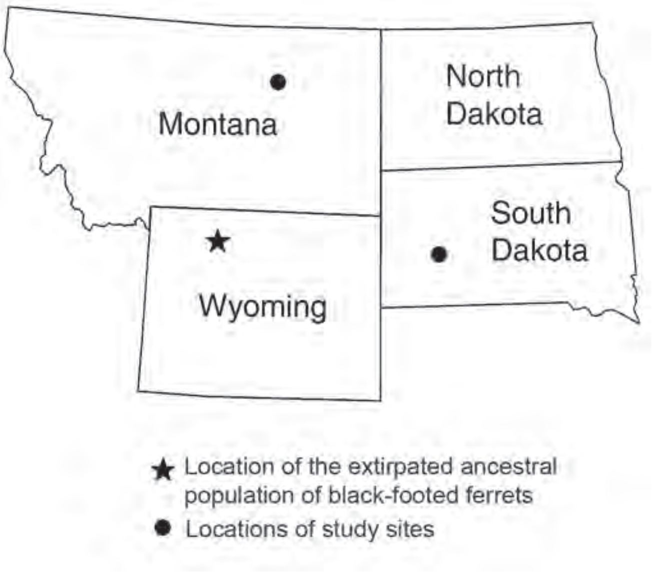

Figure 1. The site near Meeteetse, Wyo., that provided ancestral stock for the captive breeding program, and study sites in Montana and South Dakota where black-footed ferrets (*Mustela nigripes*) were released.

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use by ferrets (objective 1), habitat preferences at small scales (objective 2), and relationships between ferret territoriality and habitat quality (objective 3), all of which are relevant to ferret conservation.

Considerable evidence supports a strong relationship between prairie dogs (*Cynomys* spp.) and black-footed ferrets. A summary by Anderson and others (1986) indicates that almost all recent ferret specimens were collected from areas within the composite ranges of black-tailed prairie dogs (*C. ludovicianus*), white-tailed prairie dogs (*C. leucurus*), or Gunnison's prairie dogs (*C. gunnisoni*), and most of the explicit descriptions of locality, where provided, mentioned prairie dog colonies. The last extant ferret populations were found on prairie dog colonies, and studies of those ferrets revealed intensive use of prairie dog colonies (Hillman and others, 1979; Biggins and others, 1985). Prairie dogs are the predominant prey taken by black-footed ferrets (Sheets and others, 1972; Campbell and others, 1987). Strategies for evaluating black-footed ferret habitat (Linder and others, 1972; Forrest and others, 1985; Flath and Clark, 1986; Houston and others, 1986; Biggins and others, 1993) universally assumed that prairie dog colonies were a primary requirement. Others, however, have questioned the characterization of black-footed ferrets as extremely specialized (Owen and others, 2000). One objective of this study was to further document the use of habitats by ferrets on a large scale, using data from radio tracking and maps of black-tailed prairie dog colonies in Montana and South Dakota, to reexamine the degree of dependence of black-footed ferrets on prairie dogs.

Evaluations of ferret habitat are mostly large scale, conducted on colonies hundreds of hectares in size and on complexes occupying thousands of hectares, leaving the details of how ferrets use their local environments largely unexplored. If black-footed ferrets are obligate predators on prairie dogs and variation exists in densities of prairie dogs and their burrows within their colonies, we predict that intensity of ferret activity will correlate positively with density of prairie dogs when habitat is examined at scales smaller than colonies. Thus, our second objective was to evaluate preferences of ferrets by using sample parcels of land <1 ha in size. To address small-scale habitat preferences and the following objective, we used burrow densities as an indicator of habitat quality. Prairie dog burrow densities should give a suitable measure of habitat quality for black-footed ferrets, in part because they correlate to density of the prairie dog prey (Biggins and others, 1993) and in part because burrows have intrinsic value to ferrets as refuges from predators and adverse weather and as dens to rear young.

Black-footed ferrets, like many other mustelids, appear to be intrasexually territorial (Powell, 1979; Miller and others, 1996). In typical carnivore fashion, females attempt to control access to food resources, while males attempt to control access to females (Ewer, 1973). Although several factors in varying combinations appear to contribute to an organism's resource holding power (e.g., relative size of contestants, age, experience in former contests), prior residency often confers significant advantages. The residency advantage is widespread among several taxa, including insects (Davies, 1978), arachnids (Riechert, 1978), decapods (Jennions and Backwell, 1996), fish (Harwood and others, 2003), amphibians (Mathis and others, 2000), and mammals (Neumann, 1999). Because many of the ferrets we studied were released into unfamiliar terrain that was either unoccupied by ferrets or occupied by ferrets for known periods of time, it was possible to examine the effect of prior residency.

Release of ferrets into vacant habitat allowed us to assess the sequence of occupancy. If habitat patches are heterogeneous, the order in which they become colonized or abandoned should relate to quality of those patches as perceived by occupants (Wiens, 1976; Krohn, 1992). Ideal free distribution theory predicts such an interrelationship between population density and carrying capacity of patches in heterogeneous habitats (Fretwell and Lucas, 1970). If order of occupancy reflects quality of habitat patches, then assessment of the colonization process also may lead to improved understanding of source-sink dynamics after habitats become fully populated (Howe and others, 1991; Pulliam and Danielson, 1991). To evaluate intraspecific competition for habitat and order of occupancy of habitat patches, we again utilized radio-telemetry data, overlaying ferret locations onto digitized maps of prairie dog burrows within the colonies studied.

Methods

We radio tracked 153 black-footed ferrets on prairie dog colonies at UL Bend National Wildlife Refuge, Mont., and on the Buffalo Gap National Grassland, S. Dak., during September–November 1994–97 (figs. 1 and 2). Some of the resulting 28,560 telemetric fixes were used for multiple studies; the UL Bend data from 1994 and 1995, for example, were also used in the comparisons of adults and kits reported herein (Biggins, Godbey, Livieri, and others, this volume). We affixed transmitters having 20-cm whip antennas to wool collars of 1-cm width, using Teflon® (DuPont, Wilmington, Del.) heat-shrink tubing (Biggins and others, 1999; Biggins, Godbey, Miller, and Hanebury, this volume). We weighed and radio collared ferrets that were wild caught or captive bred (while the animals were held under isoflurane anesthesia) and inserted passive integrated transponder chips for long-term identification (Biggins, Godbey, Matchett, and others, this volume). Ferrets from captive breeding facilities were reared under a variety of strategies and released during August–November with no more than 1-day acclimation in onsite cages (Biggins and others, 1998).

We radio tracked ferrets from fixed stations fitted with dual-beam, 11-element Yagi antennas on 6-m masts and used null-peak direction finding and triangulation to fix each ferret's position at intervals of 7–60 minutes while the animals

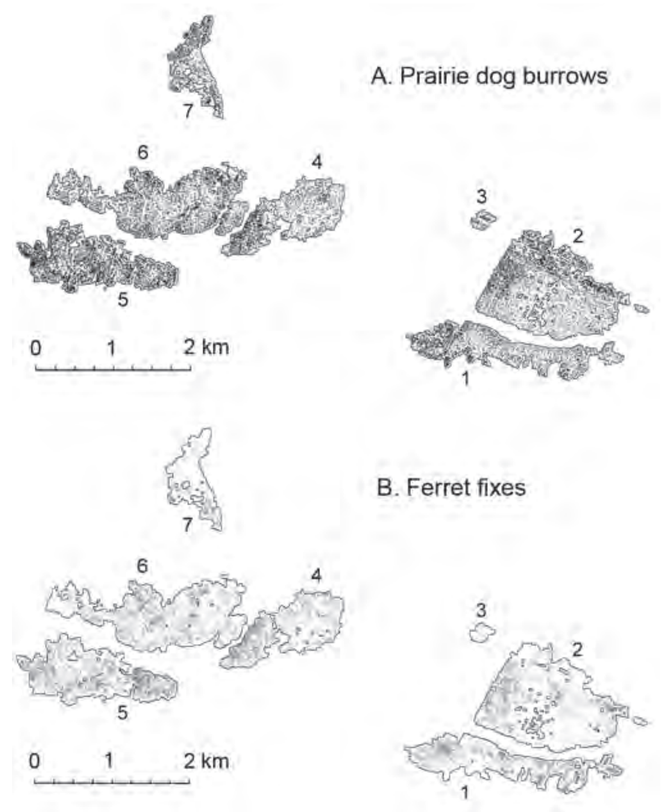

Figure 2. Distribution of black-tailed prairie dog (*Cynomys ludovicianus*) burrows (A) and black-footed ferret (*Mustela nigripes*) telemetric fixes (B) on colonies at UL Bend National Wildlife Refuge, Mont. Each dot is a burrow opening or telemetric fix; density of resulting stippling thus reflects density of burrows or fixes. Attributes for numbered colonies are summarized in table 1.

were active above ground (Biggins and others, 1999; Biggins, Godbey, Livieri, and others, this volume). We developed station-specific error estimates from test data by using differences between telemetry-derived azimuths and azimuths to transmitters of known location (Biggins and others, 1999; Biggins, Godbey, Miller, and Hanebury, this volume). Aboveground activity of black-footed ferrets is mostly nocturnal (Biggins and others, 1986; Biggins, 2000), so we limited monitoring of ferrets to hours of darkness for 2 weeks to 2 months postrelease. We recorded estimated locations of ferrets and associated error polygons as Universal Transverse Mercator coordinates derived from paired azimuths with program TRITEL (Biggins, Godbey, Miller, and Hanebury, this volume).

We recorded locations of prairie dog burrow openings (henceforth, such openings will be referred to as burrows) with Global Positioning System (GPS) receivers, differentially corrected to provide point estimates with errors of <1 m. ArcInfo® Version 8.2 (Environmental Systems Research Institute, Inc., Redlands, Calif.) was used for all vector processing, and the GRID module was used for all raster modeling. The vector point data for all prairie dog burrows and ferret locations in the study were consolidated into the Universal Transverse Mercator Zone 13 projection using the North American Datum of 1927. The GRID module was used to convert the vector points to 1-m^2 cells. To create a map of each prairie dog colony, cells were expanded by 10 m in every direction. Thus, the maps of colonies (fig. 2A,B; table 1) can be envisioned to include a buffer of 10 m beyond the outermost burrows and to exclude spaces within the outer boundary that are >10 m from the nearest burrow.

Use of Habitats Other than Prairie Dog Colonies

To investigate the broad-scale preference of black-footed ferrets for prairie dog colonies, we examined ferret use of the colonies as defined above and their use of noncolony areas. Ferret fixes were classified as being on or off colonies. Because there were nearby colonies in the South Dakota complex that were not mapped with the system described, ferret fixes that were not on mapped colonies could have been on other colonies. Thus, we did not use South Dakota data for these large-scale assessments. Similarly, a subset of ferrets in Montana (14 animals living near the eastern boundary of the subcomplex) had access to colonies that were not mapped with this system and were likewise eliminated from the analysis. The remaining data used for this overview included 24,512 fixes on 108 radio-tagged animals, including released and resident adults and kits. Because ferrets presumably must make exploratory moves to assess the distribution of prairie dogs, and because some ferrets traversed noncolony areas during routine travels between colonies, fixes that were off colonies do not necessarily imply that ferrets were actually living in areas not occupied by prairie dogs. We estimated the relative use of noncolony areas attributable to these phenomena, defining an off-colony excursion as a movement involving ≥2 fixes

Table 1. Black-tailed prairie dog (*Cynomys ludovicianus*) colonies where prairie dog burrows were mapped. Numbers for Montana colonies correspond to the numbered colonies of figure 2.

Colony	Area (ha)	Burrows/ha
Montana		
1. South Locke	90.1	57.9
2. North Locke	166.0	48.9
3. Small	5.0	64.1
4. Sagebrush	79.8	49.8
5. South Hawley	102.4	79.4
6. North Hawley	144.0	54.6
7. Wilderness	42.2	62.1
South Dakota		
North Sage Creek	160.1	138.9

away from a colony, followed by return to a colony. We also tallied the number of fixes associated with intercolony moves and dispersal moves (movement with no return to a colony).

Preferences Within Prairie Dog Colonies

We examined habitat preferences of ferrets within colonies at a small scale by comparing counts of the number of mapped burrows in circular plots of 0.07 ha (radius = 15 m) surrounding ferret fixes with counts in similar plots surrounding random points on colonies (fig. 3), sampling with replacement (plots were allowed to overlap). To be included in the analysis, the boundary of a sample plot was required to be entirely within a colony as defined above. Ferrets with ≤3 fixes were excluded. To characterize densities of prairie dog burrows on the Montana colonies, we sampled 20,328 plots at random points and compared those to plots centered on 21,185 fixes for 110 ferrets. In South Dakota, we counted burrows within plots surrounding 427 fixes (for 19 ferrets) and 465 random points. Because many ferret fixes for individual animals were serially autocorrelated (e.g., the sequential fixes of fig. 3), we summarized density of burrows within plots as mean densities for each animal and used those means in all subsequent analyses. Thus, sample sizes became numbers of animals (not numbers of fixes). We further restricted this data set to include only those ferrets radio tracked >3 days; estimates for animals radio tracked for shorter periods were deemed unreliable.

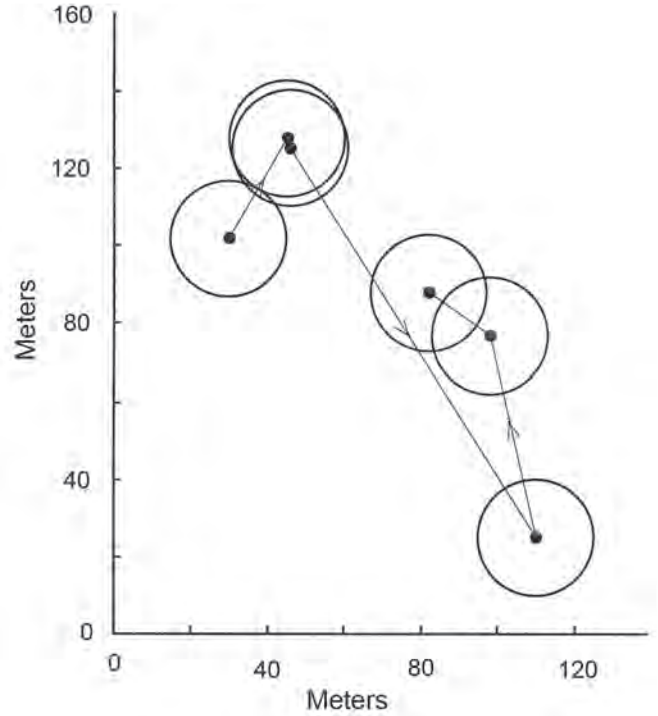

Figure 3. Example of encircling a series of telemetric fixes with plots of 15-m radius, within which black-tailed prairie dog (*Cynomys ludovicianus*) burrow entrances were counted, for black-footed ferret (*Mustela nigripes*) no. 32, North Sage Creek, S. Dak., on the night of October 26–27, 1997. Overlapping plots were allowed for both ferret fixes and random points (sampling with replacement).

A patchy distribution of habitat (burrows) within prairie dog colonies is a prerequisite for allowing choice by ferrets. Frequencies of counts within the plots described above would be expected to follow a Poisson distribution if dispersion of burrow openings on colonies were random (Ricklefs, 1990). For a Poisson distribution, the variance in counts is equal to the mean; evenly spaced burrow openings will produce a variance less than the mean, and clumped burrow openings will result in variance greater than the mean. We examined the variance:mean ratios for the counts within our samples of circular plots to provide an indication of dispersion of burrow openings in each colony.

Intraspecific Competition for Habitat

To assess intraspecific competition for habitat, we compared habitats occupied by groups of black-footed ferrets that were expected to differ in competitive standing. We predicted that (1) resident adult ferrets would have a competitive advantage over their wild-born kits, (2) wild-born kits would have an advantage compared to released kits, (3) kits released first would be more competitive than kits released subsequently into the same area in the same year, (4) larger kits would have an advantage over smaller kits, and (5) kits released into unoccupied habitat during the first year of reintroductions at a site would have an advantage over kits released in subsequent years to augment a population. As outlined above, we assumed burrow density correlated positively with habitat quality. We thus expected dominant ferrets to occupy areas of higher burrow density compared to their less competitive counterparts. We assessed burrow densities estimated from the sample of 0.07-ha plots described above.

As implied by the groups in comparisons 1–5 above, various overlapping subsets of animals were used for analyses. Montana data were best suited for this assessment because ferrets were released in multiple years on several colonies, they were released in several consecutive groups in the same colonies during 2 years, and resident ferrets were monitored during 1 year. As with the broader analysis above, we included only those ferrets radio tracked >3 days. Within the Montana data set, the comparison of adult and young resident ferrets (1 above) was limited to the 1997 subset of data collected on Hawley and associated colonies, as was the comparison of wild-born and released young ferrets (2). We compared groups of young ferrets released sequentially during the same years at the same sites (3) within the 1994 and 1995 data sets at all colonies. Measures of mass (4) were available for Montana animals released in 1994 and 1995, and that variable was included in the assessment of within-year sequential releases. Because sexes are dimorphic, we included sex in the model to interact with mass. Finally, we compared young ferrets released into vacant habitat at Hawley and associated colonies in 1995 with young ferrets released into that habitat in 1997, when portions of it were occupied by resident ferrets (5 above). That 368.3-ha area of prairie dog colonies (the four western colonies of fig. 2A,B) was occupied by at least 8 adults and 19 kits that we marked (not all were monitored via the radio tracking of this study).

To provide additional evidence on the effect of competition, we assessed numbers of released ferrets that moved between colonies in 1995, when these ferrets were released into habitat without a resident population of ferrets, and in 1997, when ferrets were released into the same prairie dog colonies to augment an existing population.

Statistical Evaluation

For statistical comparisons, we reduced burrow density data to animal-specific estimates for habitat they used, paired with colony-specific estimates for colonies they occupied. If an animal occupied more than one colony, we calculated separate pairs of estimates (use and availability) for each colony. We used multivariate general linear modeling (repeated measures) to evaluate differences between burrow densities for colonies and for habitat used by ferrets, assuming that all habitat on the colony occupied by a ferret was potentially available to that ferret. General models were reduced to more parsimonious versions by backward elimination using partial F-tests, when appropriate. Comparisons were judged as significant if the probability of committing a Type I error was ≤ 0.05. Exact chi-square analyses (Berry and Mielke, 1985) assisted in evaluation of proportions of ferrets engaging in intercolony movements.

Results

Use of Habitats Other than Prairie Dog Colonies

Of the 24,512 total fixes used, 2,744 (11.19 percent) were off colonies. There were 88 instances of intercolony movement. Some of the off-colony locations were solitary telemetric fixes that could be the result of radio-tracking error. Because clusters of sequential fixes provide information on pattern of movement, we assessed off-colony moves using groups of ≥ 2 consecutive fixes away from a colony. The number of clustered fixes off colonies was 2,010 in 474 bouts of movement made by 87 animals with 1 to 24 bouts per ferret; 1,767 of these (87.91 percent) were associated with exploratory excursions involving returns to the colony of origin (fig. 4) and intercolony moves (fig. 5). If these cluster-based estimates are applied to the total of 11.19 percent of fixes away from prairie dog colonies, it appears that only about 1.4 percent ($0.1119 * 0.1209 = 0.0135$) of the total number of off-colony fixes may involve dispersal (fig. 6) without known return to the colony of origin or travel to another colony.

Preferences Within Prairie Dog Colonies

Patchiness in dispersion of burrow openings was highly evident, as indicated by variance:mean ratios >>1.0 for all colonies (fig. 7) sampled by 0.07-ha circular plots. Overall, black-footed ferrets preferred patches of habitat with densities of prairie dog burrows higher than the averages for colonies they occupied (fig. 8). Our general statistical model evaluated overall differences between ferret plots and random plots (hereafter referred to as preference) and the effects of sex and colony. Sex accounted for relatively little variation ($F_{1,149} = 0.130$, $P = 0.719$) and was removed from the model. Preference of sites with elevated densities of burrows was consistent ($F_{1,154} = 16.996$, $P < 0.001$) among colonies (fig. 8), but the magnitude of the differences between burrow densities in

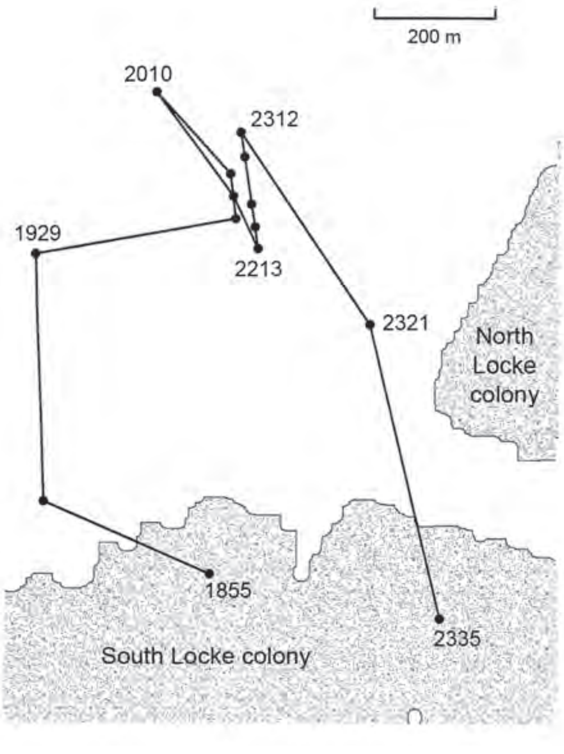

Figure 4. An example of an exploratory excursion away from a black-tailed prairie dog (*Cynomys ludovicianus*) colony by young male black-footed ferret (*Mustela nigripes*) no. 24, UL Bend National Wildlife Refuge, Mont., October 20, 1994. Numbers associated with points are times of day.

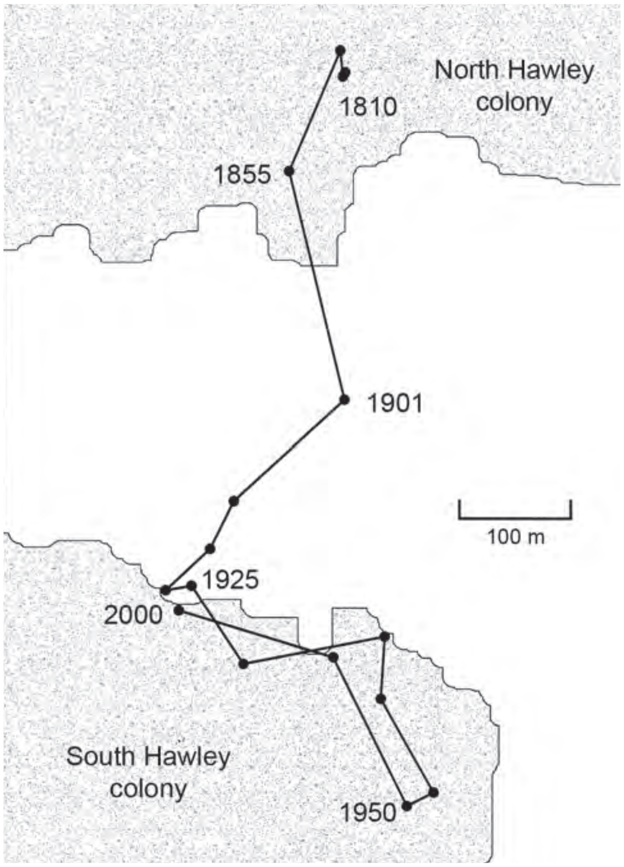

Figure 5. An example of an intercolony move by young female black-footed ferret (*Mustela nigripes*) no. 71, UL Bend National Wildlife Refuge, Mont., November 5, 1995. Numbers associated with points are times of day.

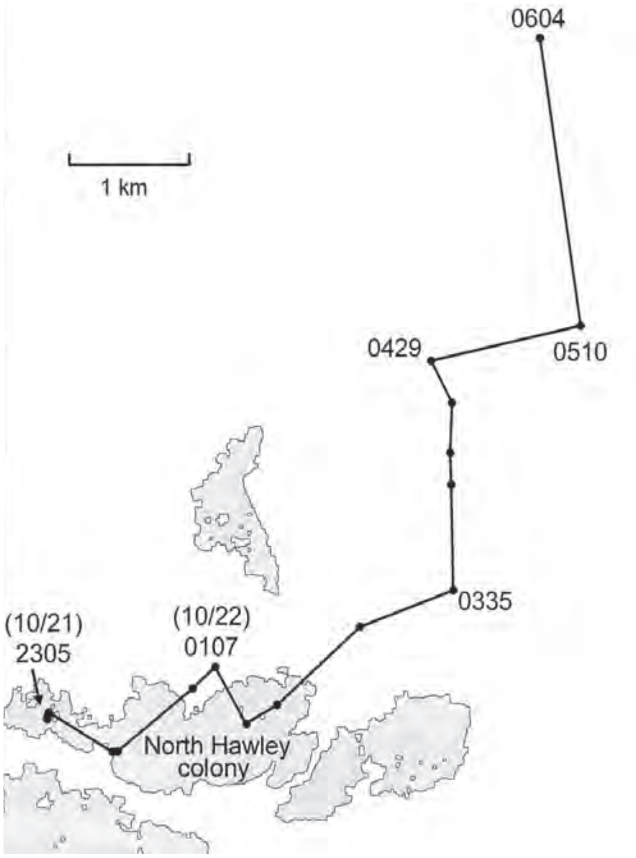

Figure 6. An example of dispersal away from black-tailed prairie dog (*Cynomys ludovicianus*) colonies by young male black-footed ferret (*Mustela nigripes*) no. 213, October 21–22, 1997. Numbers associated with points are times of day.

ferret and random plots appeared to vary (preference × colony interaction; $F_{7,154} = 2.144$, $P = 0.042$).

Intraspecific Competition for Habitat

Three of the four general models in these analyses had only class of animal in the repeated measures comparison of random and ferret-centered estimates of burrow density; these three models were not further reduced. Failure of sex and mass (in the 1994 and 1995 Montana data) to explain significant variation ($P > 0.160$) resulted in reduction of that model to a simpler submodel resembling the others used to evaluate competition. Each of these subsets of data reflected the significant habitat preferences of ferrets ($P \leq 0.010$) that were documented in the more general treatment above. Our primary focus in evaluations of competition was centered on the interaction term of each model that tested whether classes of ferrets influenced variation in differences between habitat used and habitat available (preference). In that regard, only the comparison between habitat preferences of resident adult ferrets and their resident young failed to explain significant variation (preference × age interaction; $F_{1,31} = 0.579$, $P = 0.452$). As predicted, wild-born resident young ferrets were

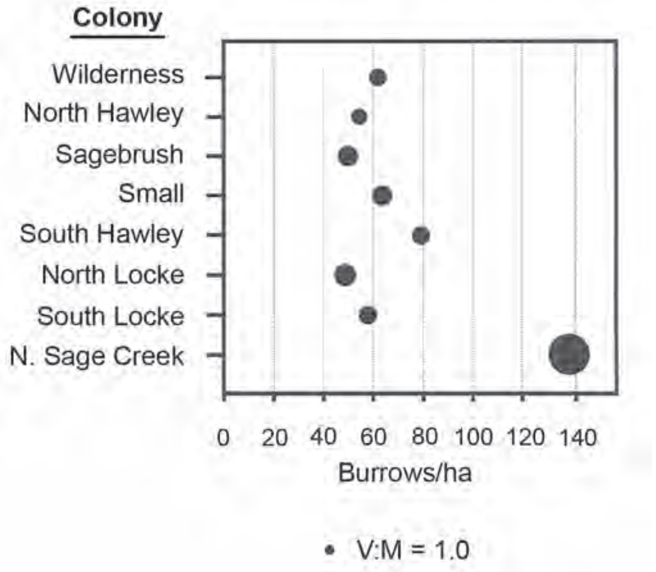

Figure 7. Densities of burrows on study colonies and variance to mean ratios (V:M) estimated from samples of 0.07-ha plots. Diameter of symbol is proportionate to V:M ratio within sample of plots.

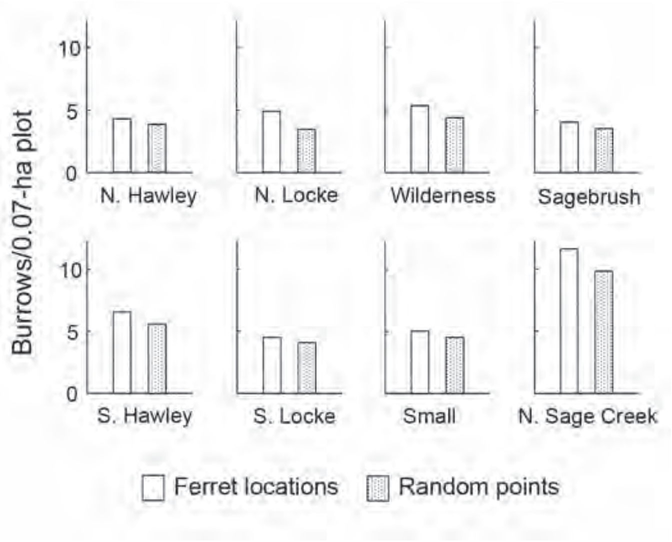

Figure 8. Burrow densities within plots encircling telemetric fixes of black-footed ferrets (*Mustela nigripes*) and within plots at random points on black-tailed prairie dog (*Cynomys ludovicianus*) colonies.

able to exercise a higher level of preference than did released young (fig. 9) (preference × origin interaction; $F_{1,51} = 4.445$, $P = 0.040$), first-released young ferrets were more selective than were young released later the same year (fig. 10) (preference × sequence interaction; $F_{1,67} = 4.430$, $P = 0.039$), and young ferrets released into vacant habitat were more selective than were young used to augment the population in that habitat during a later year (fig. 11) (preference × year interaction; $F_{1,62} = 4.063$, $P = 0.048$).

Most (12/13 = 92.3 percent) young ferrets added to the resident population in the western colonies of the UL Bend complex in 1997 moved between colonies. That proportion was significantly different ($X^2 = 13.789$, $df = 1$, $P < 0.001$) from the corresponding proportion for 1995 (8/27 = 29.6 percent), when young ferrets were released into the same colonies that were then vacant.

Discussion

Use of Habitats Other than Prairie Dog Colonies

The term “preference” suggests that use is compared to availability, but we made no explicit attempt to define or measure availability of habitat not occupied by prairie dogs. Noncolony areas, however, were much more available to ferrets (on a large scale at least) than were prairie dog colonies. Thus, the extremely high use of prairie dog colonies by black-footed ferrets does indeed suggest strong preference, and there was no need to delve into more rigorous analyses of preference at that large scale.

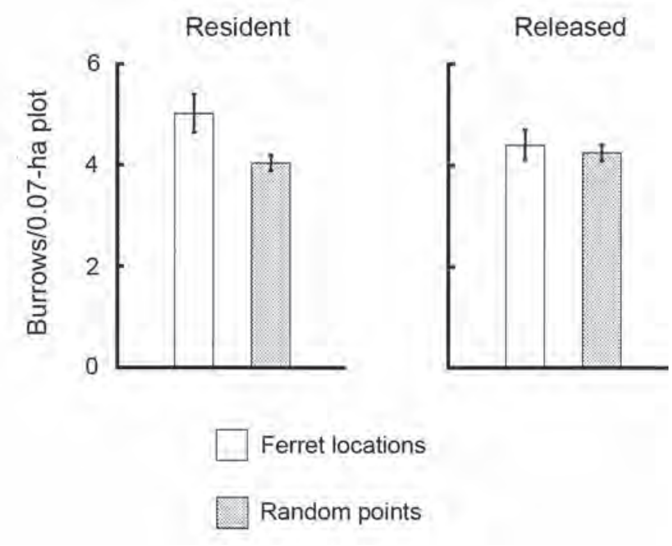

Figure 9. Densities of burrows (mean ± SE) in areas used by (and available to) black-footed ferret (*Mustela nigripes*) kits released into ferret-occupied habitat at Hawley Flats Mont., in 1997, and densities of burrows in habitat used by (and available to) the resident wild-born ferret kits at that site.

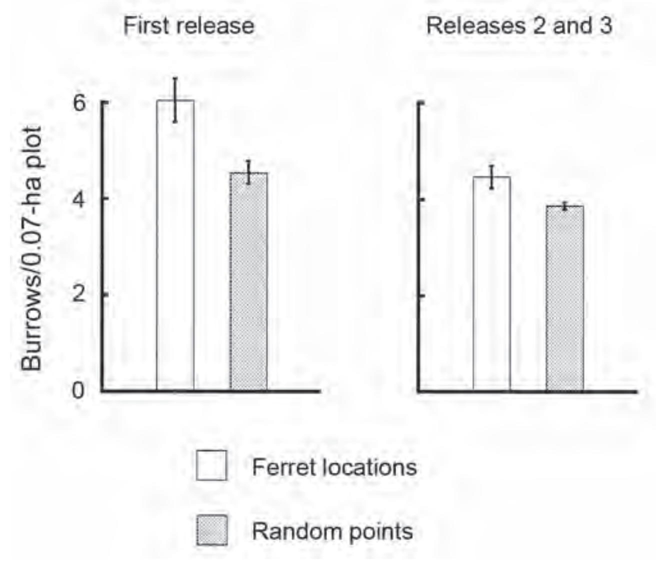

Figure 10. Densities of burrows (mean ± SE) in areas used by (and available to) the first black-footed ferret (*Mustela nigripes*) kits released at Locke Ranch and Hawley Flat, Mont., in 1994 and 1995, and densities of burrows in areas used by (and available to) ferret kits after subsequent releases during those years at those sites.

Most ferrets tracked during this study were young of the year, and many were captive-born ferrets released onto prairie dog colonies. To learn about their new surroundings, these naive animals must explore, and some may adopt home ranges that include multiple colonies. Thus, the small proportion of telemetric fixes away from prairie dog colonies is mostly explained by behaviors that should be expected even for a species fully dependent on prairie dogs. Also, a greater proportion of off-colony fixes occurred in the 1997 animals

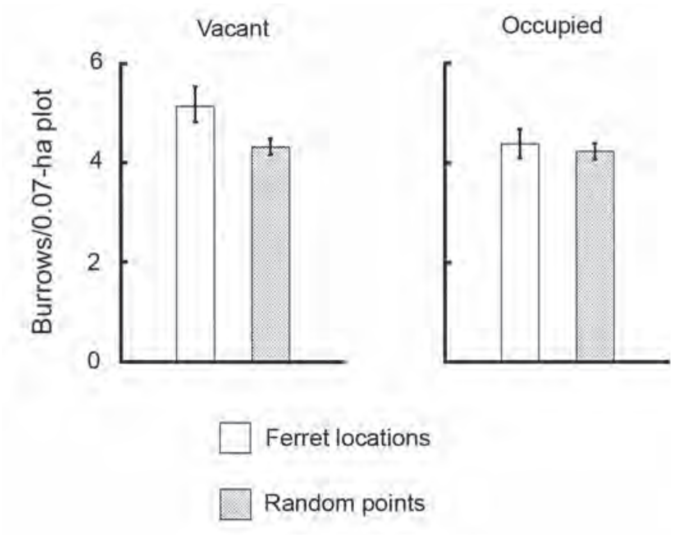

Figure 11. Densities of burrows (mean ± SE) in areas used by (and available to) black-footed ferret (*Mustela nigripes*) kits released into ferret-unoccupied habitat at Hawley Flat, Mont., in 1995, and densities of burrows in areas used by (and available to) ferret kits released to augment the extant population in 1997.

(16.7 percent), which were subjected to potentially more intense intraspecific competition than were the ferrets released into unoccupied habitat in 1994 and 1995. Considering that the remaining small proportion of "unexplained" off-colony moves also involved (1) ferrets that were killed by predators and carried away from colonies, (2) ferrets with whom telemetric contact was lost, rendering their future travels and fates unknown, (3) predominantly captive-reared ferrets that may behave erratically at times, and (4) dispersal that ultimately may lead ferrets to other prairie dog colonies, there was little indication that ferrets will attempt to live on habitat other than prairie dog colonies, let alone successfully colonize other habitats. We documented a high degree of preference for prairie dog colonies by ferrets, which weakens the contention that there should be a "broader range of possibilities for conservation of the black-footed ferret" (Owen and others, 2000, p. 422), an argument implying broader habitat tolerances based on similarities between black-footed ferrets and Siberian polecats (*Mustela eversmannii*) and the hypothetical niches of North American Pleistocene and Holocene ferrets (or polecats). Our data and those of others (e.g., Biggins, 2000) suggest that natural selection has resulted in considerable divergence of behaviors and nonskeletal features in these two extant species of *Mustela* and that they are "ecological equivalents" (Hoffman and Pattie, 1968, p. 57; Lincoln and others, 1998, p. 94) only in the broadest sense. Attempts to release each species on varying habitats further test this hypothesis. Reproductively sterile Siberian polecats persisted for only short periods when released on prairie dog colonies in Wyoming (16 percent survival for 15 days) and Colorado (16 percent survival for 1 day) (Biggins, 2000), and some of the polecats used habitats other than the prairie dog colonies. Release of Siberian polecats and black-footed ferrets into colonies of larger species of North American ground squirrels (*Spermophilus*) has not been attempted but could be informative.

Preferences Within Prairie Dog Colonies

For analyses of habitat preference within colonies, we defined as available to a ferret all of the prairie dog colony on which it resided. Definitions of availability are always somewhat arbitrary but are important because they affect the outcome of preference analyses (Johnson, 1980). Prior studies of ferret movements (Biggins and others, 1985, 1999; Biggins, 2000), coupled with the relatively small sizes of the colonies of the present study, helped justify our definition. We believe that the subjects of our study would not have been physically impeded from accessing any portion of the colonies on which they resided and were influenced primarily by the variables targeted for study (quality of habitat and competition for it). Even within the boundaries of prairie dog colonies, therefore, ferrets consistently preferred areas with relatively high densities of prairie dog burrows.

The preference of black-footed ferrets for areas on prairie dog colonies with high densities of prairie dog burrows was made possible by the clumped dispersion of burrows at our study sites. This nonrandom and nonuniform arrangement of burrow openings may be due to phenomena at several scales. Habitat quality for prairie dogs themselves may vary within the boundaries of their colonies, resulting from variation in soil type, soil depth, slope, and aspect. Vegetative mosaics are apparent on some colonies, resulting from these edaphic and physiographic attributes and other influences (e.g., plant competition) and from grazing by prairie dogs. Thus, the patchiness we observed at the scale of our plots (707 m^2) is likely a reflection of the patchiness at intermediate scales (measured in hectares) resulting from the factors mentioned above coupled with variation at finer scales caused (at least in part) by the social organization of black-tailed prairie dogs into coteries and by interconnected burrow openings within coteries (Hoogland, 1995). We believe that attention to these considerations of scale will be increasingly important in gaining a more complete understanding of ferret ecology. Former evaluations of habitat for black-footed ferrets (e.g., Hillman and others, 1979; Forrest and others, 1985; Houston and others, 1986; Miller and others, 1988; Biggins and others, 1993) heavily emphasized the larger scales of colonies and complexes and may have led us to overlook details important to ferrets. Ferret preferences for areas of relatively high densities of prairie dog burrows, and the apparent intraspecific competition for those areas, imply qualities that may be related to fitness. We hypothesize that the value of clusters of burrow openings lies not only in their correlation to clusters of prairie dogs as prey but also in the immediacy of protective cover from predators during aboveground movements by ferrets. Predation appears to be a substantial hazard for ferrets (Forrest and others, 1988; Biggins, 2000), causing by far the most losses during the repatriation program (Biggins, Godbey, Livieri, and others, this volume). Because of the positive association between safety and resources, ferrets are not forced into tradeoffs requiring choices between “a productive, but risky habitat and a less productive, safer habitat” (Grand and Dill, 1999, p. 389).

Intraspecific Competition for Habitat

Several lines of previous evidence suggest that territoriality is an important feature in the social lives of black-footed ferrets. Although direct agonistic encounters between free-ranging individual ferrets are rarely seen (Clark and others, 1986), two adult males were observed in what was described as “mortal combat” at the UL Bend in 1997 (Stoneberg, 1997, p. 13). Play behaviors in juveniles that may be precursors to such behaviors in adults (Poole, 1966, 1967, 1974) were commonly seen in free-ranging (Hillman, 1968; Clark and others, 1986) and captive (Miller, 1988; Vargas, 1994) litters. Agonistic behaviors between captive adult black-footed ferrets resembled agonistic interactions of domestic ferrets (Miller, 1988). General spacing patterns suggest that ferrets occupy somewhat distinct territories (Clark, 1989). Scent marking is a common behavior in ferrets and is particularly evident for males during the breeding season (Miller, 1988). Our understanding of competition among ferrets (especially females) for resources or space is nevertheless incomplete. Although free-ranging ferrets tend to occupy space that is not used by other ferrets of the same sex, occasional sharing of space by females during winter (Richardson and others, 1987) and even by females with litters (Paunovich and Forrest, 1987) raises doubts about exclusiveness of areas of activity. Captive Siberian polecats have been held in large cages for prolonged periods as same-sex and mixed-sex groups, but, on other occasions, aggression has been immediate and severe when multiple polecats were introduced into the same space (D. Biggins, unpub. data, 1995). Individual black-footed ferrets have severely injured their neighbors in conflicts through the wire mesh that separated their adjacent outdoor pens, and female ferrets have even killed their prospective mates (A. Vargas, oral commun., 1995). Simple rules seem inadequate for predicting outcomes of interactions. For females especially, activity area sizes and their exclusivity in time and space may be influenced by habitat quality and variation among individuals (Biggins, 2000), and perhaps nepotism at times masks the central tendency of ferrets to defend territories.

Nonetheless, the general theme of competition among black-footed ferrets for possession of space was supported by our study; the group that was predicted to be subordinate based on prior residency consistently occupied the habitat of lower quality. Large body size may be an advantage in contests, but we did not detect a significant effect of mass in the competition for high-quality habitat among sequentially released young ferrets. Ferrets seemed to follow the “bourgeois strategy” (Ramsay and Ratcliffe, 2003, p. 120) in which prior residency overwhelms effects of size and other factors. The duration of prior residency also may have an effect (Harwood and others, 2003). In an experiment involving releases of white-throated sparrows (*Zonotrichia albicollis*) into outdoor aviaries, Dearborn and Wiley (1993) noted a gradual increase in effect of prior residency from 2–45 days, but the increase was most dramatic during the first 14 days. Duration of prior residency for ferrets in our sequential release experiment was fairly brief, with 2–4 weeks between the first and subsequent releases, but duration of residency was >1 year for individuals in the extant population that was augmented in 1997.

As ferret populations are assembled through progressive releases and additions of wild-born animals, intraspecific competition appears to result in sequential occupation of habitat patches by descending order of burrow (and prey) density. As available habitat becomes filled, the additional occupancy of sites with lower densities of burrows and prairie dogs is expected to increase the variance in burrow density of occupied sites. At sites with low burrow densities, areas of activity of ferrets may be largest. These phenomena outwardly resemble the characteristics associated with an ideal free distribution or an ideal dominance (despotic) distribution (Fretwell and Lucas, 1970). Explorations by released ferrets may be sufficient to impart “ideal” knowledge regarding availability of habitat, but territoriality of resident ferrets may prevent “free” choice (sensu Fretwell and Lucas, 1970). Further assessment of processes involved in ferret habitat occupancy in relation to theoretical distributions (Fretwell and Lucas, 1970; Fretwell, 1972) must consider relative fitness (Messier and others, 1990; Beckman and Berger, 2003), a topic we will address separately with other data sets.

Commonly used habitat evaluation systems for black-footed ferrets (e.g., that of Biggins and others, 1993) likely overestimate ferret densities attainable on the best habitats. As acknowledged by Biggins and others (1993, p. 75) in the introduction to their suggested model, “Social behavior may dictate a maximum ferret density regardless of prey abundance.” Mounting evidence regarding territoriality in ferrets does indeed suggest that models used to predict carrying capacity of habitat for ferrets should include an increasing effect of social exclusion of ferrets at high densities of prairie dogs. Because the best quality habitats as rated by the model of Biggins and others (1993) are presently sustaining ferrets at densities almost double those of low-quality habitats, we suggest retention of the fundamental structure of the model, with modifications recently suggested (Biggins, Lockhart, and Godbey, this volume). Although our comparative data suggest that competitiveness varies among individuals and has an important influence on population assembly (groups varied in their ability to control space and resources), we are unable to estimate the strength of territoriality at varying prey densities.

Additional studies on territoriality in male and female ferrets could help refine predictions of the model at high prairie dog densities. The model also would benefit from an improved understanding of habitat limitations for reproductive female ferrets inhabiting colonies with low prairie dog densities, a subject beyond the scope of this study.

The prior residency advantage raises other issues of conservation concern. Quality of ferrets released may vary because of prerelease experience (Biggins and others, 1998, 1999) and age (Biggins, Godbey, Livieri, and others, this volume). Preliminary releases of lower quality animals may reduce the amount of good habitat available for higher quality animals subsequently released if the first animals become established. Even if those first residents succumb rather quickly to predation, their initial presence could elevate the risk to newcomers during the first critical days postrelease. Thus, we recommend careful consideration be given to choice of sites and sequence of release when habitat will receive groups of ferrets varying in prerelease experience, origin, and age.

Acknowledgments

Although space prevents us from individually recognizing the more than 40 technicians who radio tracked black-footed ferrets during these studies, we are grateful for their dedication to those long hours of nocturnal monotony punctuated with brief bouts of pandemonium. Funding was provided by the Legacy Program of the U.S. Department of Defense; U.S. Fish and Wildlife Service (FWS); U.S. Forest Service; U.S. Geological Survey; Montana Department of Fish, Wildlife and Parks; National Biological Service; National Fish and Wildlife Foundation; National Park Service; South Dakota Department of Game, Fish and Parks; U.S. Air Force; U.S. Army; and Wildlife Preservation Trust International (now Wildlife Trust). We appreciate the assistance from Project Lighthawk in moving ferrets from Pueblo, Colo., to Montana. We are deeply indebted to those who raised black-footed ferrets for the reintroduction efforts, including individuals at the Black-footed Ferret Conservation Center (FWS and Wyoming Game and Fish Department), National Zoo, Henry Doorly Zoo, Louisville Zoo, Phoenix Zoo, Toronto Zoo, Cheyenne Mountain Zoo, and the Pueblo experimental rearing facility (FWS). Additional efforts were required by dedicated individuals who preconditioned ferrets at F.E. Warren Air Force Base, Wyo., and Buffalo Gap National Grassland, S. Dak. We appreciate the assistance of B. Waltermire and D. Schneider with GIS analysis of the prairie dog burrow data. Our generic list of agencies and institutions seems inadequate to acknowledge the hundreds of individuals who accomplished the multitude of tasks necessary to produce these ferrets and move them back to their native habitats. The teamwork and coordination were mind boggling. We extend genuine appreciation to all, admitting that this is a paltry tribute for accomplishment of such a monumentally important task.

References Cited

Anderson, E., Forrest, S.C., Clark, T.W., and Richardson, L., 1986, Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851: Great Basin Naturalist Memoirs No. 8, p. 11–62.

Beckman, J.P., and Berger, J., 2003, Using black bears to test ideal-free distribution models experimentally: Journal of Mammalogy, v. 84, p. 594–606.

Berry, K.J., and Mielke, P.W., Jr., 1985, Subroutines for computing exact Chi-square and Fisher’s exact probability tests: Education and Psychological Measurement, v. 45, p. 153–159.

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Biggins, D.E., Schroeder, M., Forrest, S., and Richardson, L., 1985, Movements and habitat relationships of radio-tagged black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 11.1–11.17.

Biggins, D.E., Schroeder, M.H., Forrest, S.C., and Richardson, L., 1986, Activity of radio-tagged black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 135–140.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Campbell, T.M., III, Clark, T.W., Richardson, L., Forrest, S.C., and Houston, B.R., 1987, Food habits of Wyoming black-footed ferrets: American Midland Naturalist, v. 117, p. 208–210.

Clark, T.W., 1989, Conservation biology of the black-footed ferret *Mustela nigripes*: Philadelphia, Pa., Wildlife Preservation Trust International, Wildlife Preservation Trust Special Scientific Report No. 3, 175 p.

Clark, T.W., Richardson, L., Forrest, S.C., Casey, D.E., and Campbell, T.M., III, 1986, Descriptive ethology and activity patterns of black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 115–134.

Davies, N.B., 1978, Territorial defence in the speckled wood butterfly (*Pararge aegeria*)—the resident always wins: Animal Behaviour, v. 26, p. 138–147.

Dearborn, D.C., and Wiley, R.H., 1993, Prior residence has a gradual influence on dominance in captive white-throated sparrows: Animal Behaviour, v. 46, p. 39–46.

Ewer, R.F., 1973, The carnivores: Ithaca, N.Y., Cornell University Press, 494 p.

Flath, D.L., and Clark, T.W., 1986, Historic status of black-footed ferret habitat in Montana: Great Basin Naturalist Memoirs No. 8, p. 63–71.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Forrest, S.C., Clark, T.W., Richardson, L., and Campbell, T.M., III, 1985, Black-footed ferret habitat—some management and reintroduction considerations: Cheyenne, Wyoming BLM Wildlife Technical Bulletin No. 2, 49 p.

Fretwell, S.D., 1972, Populations in a seasonal environment: Princeton, N.J., Princeton University Press, Monographs in Population Biology 5, 217 p.

Fretwell, S.D., and Lucas, H.L., 1970, On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development: Acta Biotheoretica, v. 19, p. 16–36.

Grand, T.C., and Dill, L.M., 1999, Predation risk, unequal competitors and the ideal free distribution: Evolutionary Ecology Research, v. 1, p. 389–409.

Harwood, A.J., Griffiths, S.W., Metcalfe, N.B., and Armstrong, J.D., 2003, The relative influence of prior residency and dominance on the early feeding behaviour of juvenile Atlantic salmon: Animal Behaviour, v. 65, p. 1141–1149.

Hillman, C.N., 1968, Field observations of black-footed ferrets in South Dakota: Transactions of the North American Wildlife and Natural Resources Conference, v. 33, p. 433–443.

Hillman, C.N., Linder, R.L., and Dahlgren, R.B., 1979, Prairie dog distributions in areas inhabited by black-footed ferrets: American Midland Naturalist, v. 102, p. 185–187.

Hoffman, R.S., and Pattie, D.L., 1968, A guide to Montana mammals: Missoula, University of Montana, 133 p.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing mammal: Chicago, University of Chicago Press, 557 p.

Houston, B.R., Clark, T.W., and Minta, S., 1986, Habitat suitability index model for the black-footed ferret—a method to locate transplant sites: Great Basin Naturalist Memoirs No. 8, p. 99–114.

Howe, R.W., Davis, G.J., and Mosca, V., 1991, The demographic significance of ‘sink’ populations: Biological Conservation, v. 57, p. 239–255.

Jennions, M.D., and Backwell, P.R.Y., 1996, Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*: Biological Journal of the Linnean Society, v. 57, p. 293–306.

Johnson, D.H., 1980, The comparison of usage and availability measurements for evaluations of resource preference: Ecology, v. 61, p. 65–71.

Krohn, W.B., 1992, Sequence of habitat occupancy and abandonment—potential standards for testing habitat models: Wildlife Society Bulletin, v. 20, p. 441–444.

Lincoln, R., Boxshall, G., and Clark, P., 1998, A dictionary of ecology, evolution, and systematics: United Kingdom, Cambridge University Press, 361 p.

Linder, R.L., Dahlgren, R.B., and Hillman, C.N., 1972, Black-footed ferret–prairie dog interrelationships, *in* Symposium on rare and endangered wildlife of the Southwestern United States: Santa Fe, New Mexico Department of Game and Fish, p. 22–37.

Mathis, A., Schmidt, D.W., and Medley, K.A., 2000, The influence of residency status on agonistic behavior of male and female Ozark zigzag salamanders *Plethodon angusticlavius*: American Midland Naturalist, v. 143, p. 245–249.

Messier, F.J., Virgl, A., and Marinelli, L., 1990, Density-dependent habitat selection in muskrats—a test of the ideal free distribution model: Oecologia, v. 84, p. 380–385.

Miller, B., Reading, R.P., and Forrest, S., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Miller, B.J., 1988, Conservation and behavior of the endangered black-footed ferret (*Mustela nigripes*) with a comparative analysis of reproductive behavior between the black-footed ferret and the congeneric domestic ferret (*Mustela putorius furo*): Laramie, University of Wyoming, Ph.D. dissertation, 195 p.

Miller, B.J., Menkens, G.E., and Anderson, S.H., 1988, A field habitat model for black-footed ferrets, *in* Uresk, D.W., Schenbeck, G.L., and Cefkin, R., technical coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings: USDA Forest Service, General Technical Report RM-154, p. 98–102.

Neumann, D.R., 1999, Agonistic behavior in harbor seals (*Phoca vitulina*) in relation to the availability of haul-out space: Marine Mammal Science, v. 15, p. 505–525.

Owen, P.R., Bell, C.J., and Mead, E.M., 2000, Fossils, diet, and conservation of black-footed ferrets (*Mustela nigripes*): Journal of Mammalogy, v. 81, p. 422–433.

Paunovich, R., and Forrest, S.C., 1987, Activity of a wild black-footed ferret litter: Prairie Naturalist, v. 19, p. 159–162.

Poole, T., 1966, Aggressive play in polecats: Symposia of the Zoological Society of London, v. 18, p. 23–44.

Poole, T., 1967, Aspects of aggressive behavior in polecats: Zeitschrift für Tierpsychology, v. 24, p. 351–369.

Poole, T., 1974, Detailed analysis of fighting in polecats, Mustelidae, using cine film: Journal of the Zoological Society of London, v. 173, p. 369–393.

Powell, R.A., 1979, Mustelid spacing patterns—variations on a theme by *Mustela*: Zeitschrift für Tierpsychology, v. 50, p. 153–165.

Pulliam, H.R., and Danielson, B.J., 1991, Sources, sinks, and habitat selection—a landscape perspective on population dynamics: The American Naturalist, v. 137, p. S50–S66.

Ramsay, S.M., and Ratcliffe, L.M., 2003, Determinants of social rank in female black-capped chickadees (*Poecile atricapilla*): Canadian Journal of Zoology, v. 81, p. 117–121.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming (USA): American Midland Naturalist, v. 117, p. 225–239.

Ricklefs, R.E., 1990, Ecology (3d ed.): New York, W.H. Freeman and Company, 896 p.

Riechert, S.E., 1978, Games spiders play—behavioural variability in territorial disputes: Behavioural Ecology and Sociobiology, v. 3, p. 135–162.

Sheets, R.G., Linder, R.L., and Dahlgren, R.B., 1972, Food habits of two litters of black-footed ferrets in South Dakota: American Midland Naturalist, v. 87, p. 249–251.

Stoneberg, R., 1997, Montana black-footed ferret reintroduction program: 1996–1997 progress report: Helena, Montana Department of Fish, Wildlife and Parks, 21 p.

Vargas, A., 1994, Ontogeny of the endangered black-footed ferret (*Mustela nigripes*) and effects of captive upbringing on predatory behavior and post-release survival: Laramie, University of Wyoming, Ph.D. dissertation, 272 p.

Wiens, J.A., 1976, Population responses to patchy environments: Annual Review of Ecology and Systematics, v. 7, p. 81–120.


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Evaluating Habitat for Black-footed Ferrets: Revision of an Existing Model

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Abstract

Black-footed ferrets (*Mustela nigripes*) are highly dependent on prairie dogs (*Cynomys* spp.) as prey, and prairie dog colonies are the only known habitats that sustain black-footed ferret populations. An existing model used extensively for evaluating black-footed ferret reintroduction habitat defined complexes by interconnecting colonies with 7-km line segments. Although the 7-km complex remains a useful construct, we propose additional, smaller-scale evaluations that consider 1.5-km subcomplexes. The original model estimated the carrying capacity of complexes based on energy requirements of ferrets and density estimates of their prairie dog prey. Recent data have supported earlier contentions of intraspecific competition and intrasexual territorial behavior in ferrets. We suggest a revised model that retains the fixed linear relationship of the existing model when prairie dog densities are <18/ha and uses a curvilinear relationship that reflects increasing effects of ferret territoriality when there are 18–42 prairie dogs per hectare. We discuss possible effects of colony size and shape, interacting with territoriality, as justification for the exclusion of territorial influences if a prairie dog colony supports only a single female ferret. We also present data to support continued use of active prairie dog burrow densities as indices suitable for broad-scale estimates of prairie dog density. Calculation of percent of complexes that are occupied by prairie dog colonies was recommended as part of the original habitat evaluation process. That attribute has been largely ignored, resulting in rating anomalies.

Keywords: black-footed ferret, burrows, carrying capacity, competition, *Cynomys*, energy, habitat, *Mustela nigripes*, prairie dog, territory

Introduction

By 1988, captive breeding of black-footed ferrets (*Mustela nigripes*) rescued from a failing population in Wyoming was becoming successful (Biggins and others, 1997), and a subcommittee of the Black-footed Ferret Interstate Coordinating Committee (ICC) addressed the challenge of locating, evaluating, and comparing sites for black-footed ferret reintroduction. Habitat for terrestrial species, including prairie dogs (*Cynomys* spp.), is commonly evaluated with respect to vegetative and physiographic features. Although we recognize the crucial link between prairie dogs and their environments, the extreme specialization of the black-footed ferret allows us to equate black-footed ferret habitat with prairie dog colonies. A habitat model now in common use was developed by the ICC to assess the ability of prairie dog colonies and complexes to support populations of black-footed ferrets (Biggins and others, 1993). The model arose from earlier descriptions and models of ferret habitat (Linder and others, 1972; Hillman and others, 1979; Forrest and others, 1985; Houston and others, 1986; Miller and others, 1988), models of ferret energetics (Stromberg and others, 1983; Powell and others, 1985), data on ferret nutrition and food habits (Sheets and others, 1972; Campbell and others, 1987; Joyce, 1988), and information on behaviors of free-ranging ferrets (Hillman, 1968; Biggins and others, 1985; Paunovich and Forrest, 1987; Richardson and others, 1987). Biggins and others (1993) also provided a method for estimating approximate densities of prairie dogs from strip transect samples of active burrows and offered a technique for grouping colonies into complexes. Complexes were defined as clusters of colonies that could be circumscribed with 7-km line segments; colonies are sequentially added to a complex if they are separated by ≤7 km. Spaces within a complex that are devoid of prairie dogs are defined similarly.

We herein suggest changes to procedures described by Biggins and others (1993), based in part on information collected during 1991–2003 from reintroduced populations of black-footed ferrets, and we discuss aspects of the existing system needing renewed emphasis. Changes include assessing portions of complexes at a smaller scale (called subcomplexes), incorporating the effects of ferret territoriality

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in assessments of habitat carrying capacity, and limiting the effect of ferret territoriality on small habitat patches where social strife is unlikely to influence ferret use.

Subcomplexes

The initial impetus for considering smaller, more compact clusters of prairie dog colonies as subcomplexes stemmed from de facto procedures used to select and prioritize ferret release sites. Sites were intuitively regarded as high quality if colonies were closely spaced or large and if prairie dog densities were high. Release of ferrets took place on such “core” sites, with much less attention given to the remainder of the complex as defined by the 7-km procedure (Biggins and others, 1993). We describe a process, involving subcomplexes, that has been in practical use since 1999 by the U.S. Fish and Wildlife Service and partners to allocate ferrets.

On occasion, more than one cluster of colonies has been used as a release site, but ferret releases in each year have been conducted on relatively small portions of complexes. Following initial release(s), ferrets rather quickly populated some of these core release areas through natural reproduction; other clusters in a complex defined with the 7-km criterion were mostly populated with additional releases (e.g., Conata Basin, S. Dak.) or natural dispersal over longer time periods (Shirley Basin, Wyo.). Although lines of delineation are arbitrary, ferret movement within clusters where colonies were separated by ≤1.5 km was common. At UL Bend National Wildlife Refuge, Mont., for example, there were 88 intercolony moves by radio-tagged ferrets during 1994, 1995, and 1997 (Biggins, Godbey, Matchett, and Livieri, this volume); 77 (85.5 percent) of these moves were between colonies separated by <1.5 km, but all moves were between colonies separated by <2.1 km. In the Meeteetse, Wyo., complex of white-tailed prairie dogs (*Cynomys leucurus*) that supported the remnant ancestral population of ferrets, most colonies were interconnected with a 1.5-km maximum distance between them. Based on these experiences and data, we propose defining a subcomplex as a group of colonies that can be linked to one another with a series of line segments ≤1.5 km in length. The procedure for outlining a subcomplex will be further standardized by following the method used to circumscribe a complex (Biggins and others, 1993), but substituting a 1.5-km line segment for the 7-km line segment (fig. 1).

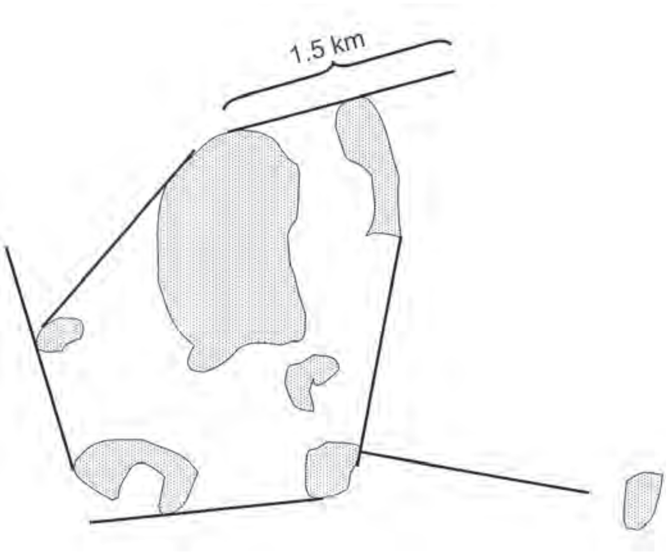


Figure 1. Procedure for circumscribing a subcomplex of prairie dog (*Cynomys* spp.) colonies by using a minimum intercolony distance of 1.5 km. See Biggins and others (1993) for additional details on the methodology.

Territoriality and Carrying Capacity

Carrying capacity has been traditionally discussed in terms of populations of an organism and their food supply, with implications of sustainability of resources (Leopold, 1933). In that sense, the habitat model of Biggins and others (1993) attempts to estimate carrying capacity of prairie dog colonies for black-footed ferrets. Many organisms, however, seem to space themselves within habitat. Carnivores are often intrasexually territorial, but King’s (1990) chapter on “adjustable living spaces” provides evidence that there is an interaction between habitat quality (mainly abundance of prey) and territoriality for other *Mustela* species. The utility of estimating the upper limits of habitat to sustain organisms, whether such limits are imposed by food or other mechanisms, was evident in early attempts to model regulated growth with the logistic equation (Pearl and Reed, 1920) and in Leopold’s (1933) discussions of managing game for sustained yields. More recent efforts at modeling ferret population fluctuations require similar input (Bevers and others, 1997).

Although somewhat conflicting evidence precluded considering ferret territoriality in their earlier model, Biggins and others (1993, p. 75) suggested that “social behavior may dictate a maximum ferret density regardless of prey abundance.” There is increasing evidence that black-footed ferret territoriality does indeed constrain predictions of the energetics model when prey may not be limiting. First, reintroduced ferret populations in South Dakota habitats seldom had average densities exceeding about 1 female per 30 ha, even though the energetics-based model often predicted 1 female per 20 ha or less. Additional evidence from ferrets released in Montana and South Dakota suggests that there is competition for good quality habitat (Biggins, Godbey, Matchett, and Livieri, this volume). These recent results are consistent with observations that female ferrets generally do not use overlapping areas (Richardson and others, 1987) and evidence of spacing in other *Mustela* species (Powell, 1979; King, 1990). The mounting evidence is sufficiently compelling that we here suggest adding a function to the simple linear relationship between densities of black-footed ferrets and prairie dogs that will have increasing impact as ferret density rises. A guiding principle is parsimony; we do not suggest adding complexity that is unsupported empirically.

We revised the energetics-based model (Biggins and others, 1993) to allow an effect of territoriality that is initiated at densities of 18 prairie dogs per hectare, gradually increases in intensity, and reaches an asymptote of 0.04 ferret families per hectare at a prairie dog density of 42/ha (fig. 2). Because a black-footed ferret family includes one female, we are discussing female ferret density. A quadratic equation ($Y = a + bX + cX^2$) adequately approximates the proposed curvilinear relationship within the range 18–42 prairie dogs per hectare, where: Y = predicted density of female ferrets, X = density of prairie dogs, a = -0.00456329, b = 0.00193283, and c = -0.00002083. If there are <18 prairie dogs per hectare, the equation for the straight line segment of the graph remains $Y = 0.00131062X$, a slope determined by the existing energetically based estimates and a linear relationship between ferret density and prairie dog density. Although white-tailed prairie dogs occasionally have been found at densities >20/ha, the graph suggests (correctly, we believe) that density of female ferrets seldom will be limited by territoriality on white-tailed prairie dog habitat. In contrast, we believe that territorial behavior of female ferrets will commonly influence their spacing on most black-tailed prairie dog (*Cynomys ludovicianus*) habitat. Under our proposed relationship, that influence will increase until female ferrets reach densities of about 1 ferret per 25 ha of habitat (the maximum density of 0.04 ferrets per hectare). We predict that prairie dog densities above 42/ha will not result in increased densities of territorial female ferrets, but these higher densities of prairie dogs may affect other population attributes such as ferret survival and productivity.

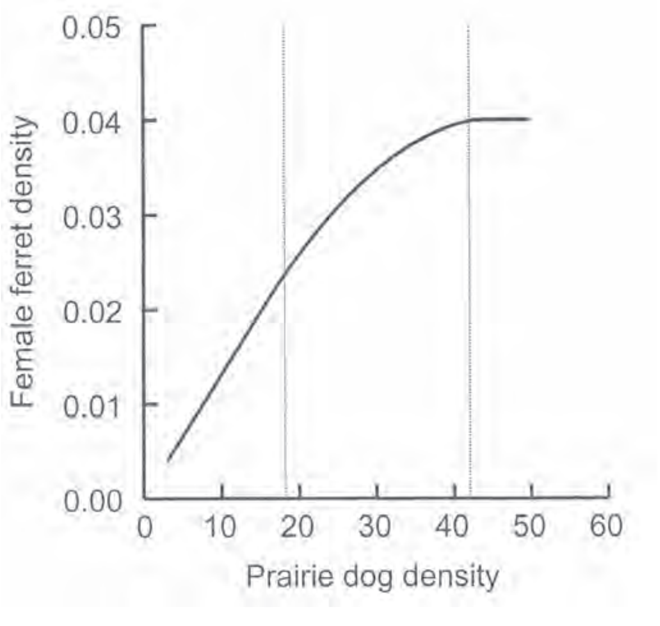


Figure 2. Hypothetical relationship between densities of prairie dogs (*Cynomys* spp.) and densities of female black-footed ferrets (*Mustela nigripes*) (individuals/ha), allowing territoriality to modify the linear relationship predicted by the energetics-based equation ($Y = X/763$) of Biggins and others (1993) at prairie dog densities >18/ha but defining an upper limit of 0.04 ferrets/ha. At intermediate prairie dog densities (18–42/ha), the increasing influence of territoriality is approximated by the quadratic equation $Y = a + bX + cX^2$, where Y = density of ferrets, X = density of prairie dogs, a = -0.00456329, b = 0.00193283, and c = -0.00002083.

Habitat-induced Isolation

"Islands" or "peninsulas" of habitat with high densities of prairie dogs may support more ferret families than would large blocks of uniform habitat because some configurations of habitat can reduce among-female interaction. An "island" arrangement with a colony small enough to support just one female and her litter (figs. 3 and 4) seems likely to eliminate any potential for limiting effects of territoriality. A "peninsula" configuration removes that effect on two sides, but territorial spacing comes into play for end-to-end territories along linear habitat. The example of 20 ha of prairie dog colony needed to support a female and her litter (fig. 3) is somewhat conservative. Five of the nine ferret litters reported by Hillman and others (1979) in Mellette County, S. Dak., were raised on colonies <16 ha in area (one was 10 ha). A female ferret raised two kits on a 5-ha colony in Montana (fig. 4); however, it seems doubtful that the Montana female could have accomplished that feat without seriously depleting the prairie dog population, and her small litter suggests that conditions may have been suboptimal. At Meeteetse, Wyo., the smallest colonies that supported females with litters were about 50 ha, but white-tailed prairie dogs at Meeteetse occurred at much lower densities (about 7.7/ha, calculated from the visual count density of Clark and others (1985) divided by the sightability adjustment of 0.495 of Biggins and others (1993)) than did the black-tailed prairie dogs discussed above (Hillman and Linder, 1973). We accommodate the most extreme of these influences of colony sizes and shapes into the evaluation procedure with a provision that removes the effect of territoriality if a colony is sufficiently small and isolated to support just a single female. To facilitate evaluation of prairie dog complexes as habitat for black-footed ferrets, a spreadsheet with appropriate formulae is available from the authors.

Colonies as small as the minimum mapping unit (5 ha) suggested by Biggins and others (1993) may support a female and her litter. Usually, however, colonies <10 ha will not have sufficient numbers of prairie dogs to sustain both themselves and a ferret family. Depletion of prairie dogs can be expected on colonies <10 ha if they are occupied by a ferret family, and it seems unlikely that such small colonies will support ferret reproduction in consecutive years. Nevertheless, we propose allowing colonies as small as 5 ha to contribute to the family rating of a complex by using the direct linear equation (Biggins and others, 1993), without the influence of

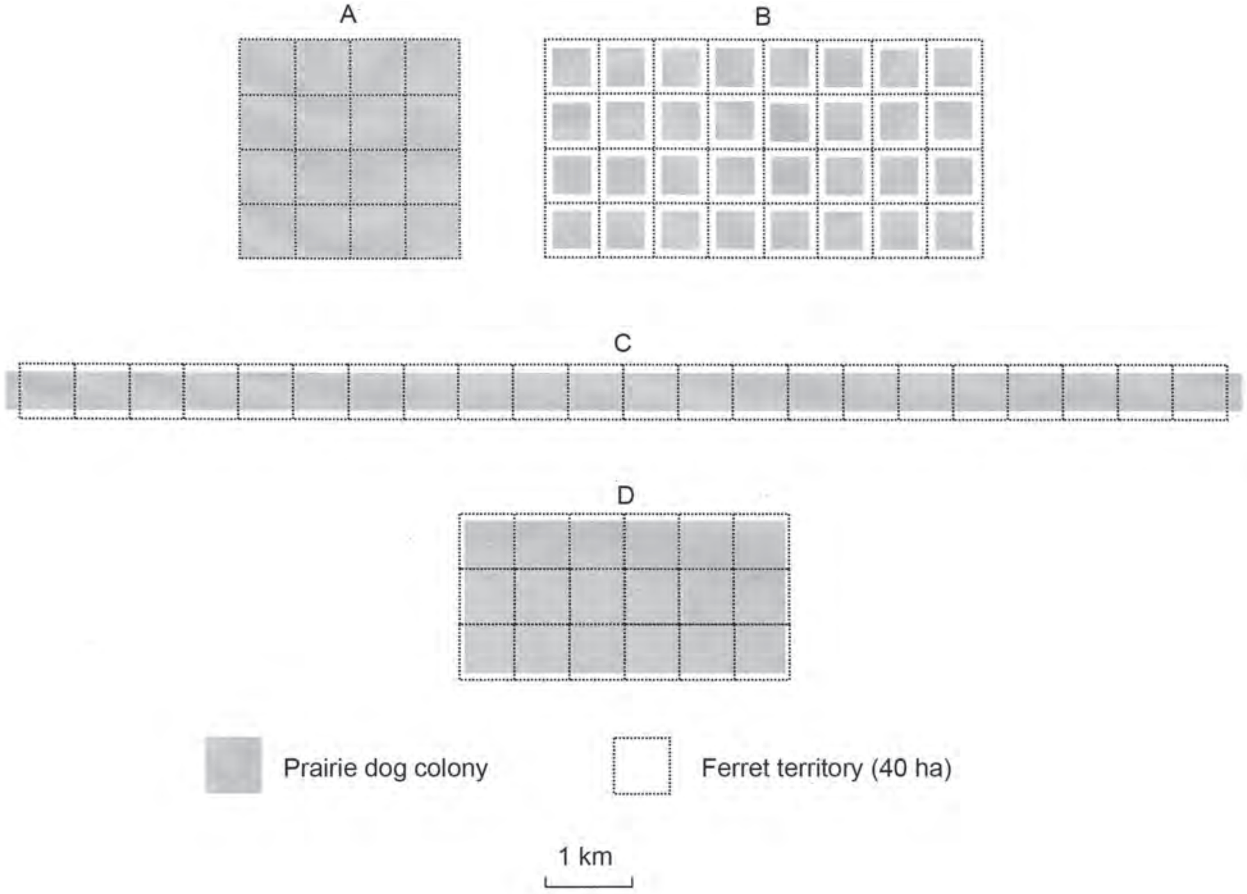


Figure 3. Comparison of female black-footed ferret (*Mustela nigripes*) numbers supported by hypothetical prairie dog (*Cynomys* spp.) complexes occupying 640 ha: (A) a complex with a single square colony ($n = 16$ ferrets); (B) a complex with 20-ha colonies at sufficient spacing to allow separate ferret territories ($n = 32$ ferrets); (C) a complex with a single linear colony (22 ferrets); and (D) a complex with a single rectangular colony (18 ferrets). These predictions are based on the following assumptions: (1) ferret territories are 40-ha squares, (2) a patch of prairie dog habitat occupying at least 20 ha is centered in the territory, and (3) a habitat patch of 20 ha has sufficient prairie dogs to sustain a ferret family while maintaining its prairie dog population.

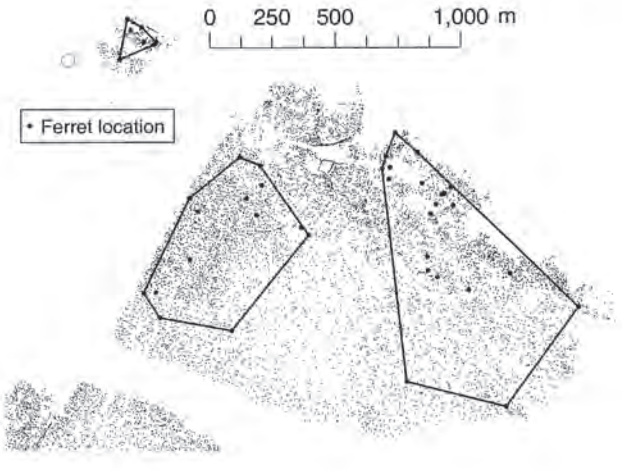


Figure 4. Activity areas (circumscribed by minimum convex polygons) for three female black-footed ferrets (*Mustela nigripes*) with litters. These females and their litters were repeatedly relocated during summer 1998 at UL Bend National Wildlife Refuge, Mont. Heterogeneity in dispersion of black-tailed prairie dog (*Cynomys ludovicianus*) burrows (small dots) is evident. The female ferret on the small colony is relatively insulated from repeated contact with other females. In this example, areas of dense prairie dog burrows do not form true “islands” of good habitat, but low densities of prairie dog burrows in the central portion of the larger colony may have influenced separation of ferret activity areas.

territoriality. If the rating using the linear equation is less than two female ferrets, then a single colony, regardless of size or prairie dog density, may be evaluated with the linear relationship (even if the result is a rating <1.0).

The concept of islands and peninsulas discussed above creates an image of prairie dog colonies within landscapes that have areas devoid of prairie dogs. Islands with high densities of prairie dogs, however, may also be situated within intervening habitat of low prairie dog density. Thus, the island effect may be operative within colonies that have heterogeneous densities of prairie dogs. The mosaic of prairie dog densities is reflected by nonuniform densities of prairie dog burrows. Heterogeneity in distribution of burrows may influence separation of activity areas of at least some female ferrets (fig. 4).

Another Look at Burrow Densities as Indicators of Prairie Dog Density

Biggins and others (1993) suggested that densities of active burrows were significantly correlated with densities of prairie dogs determined from visual counts. Severson and Plumb (1998, p. 864), however, failed to detect a relationship between densities of prairie dogs and their burrows, concluding that “burrow counts . . . should not be used to estimate or index prairie dog numbers.” This theme has a rather long history of debate extending to species other than prairie dogs, and a full discussion is outside the intended scope of this paper. Nevertheless, an overview of the topic and brief discussion of the specific criticism noted above are appropriate because working groups responsible for monitoring ferret reintroduction sites have made wide use of burrow sampling to calculate indices of habitat quality for ferrets. The need remains for a practical technique to monitor prairie dog status and trends over large scales of space (thousands of hectares) and time (decades). Decisions to use some form of capture-recapture method, visual counts, or burrow indices to estimate prairie dog abundance and density depend in part on objectives and available resources (Biggins and others, 2006). In addition, choice of method will be affected by precision and accuracy required.

Biggins and others (1993) provided only correlation coefficients for regression relationships between data from burrow transects and visual counts. To enhance comparisons with other data sets, more information is needed. Their data sets were generated from counts and transects on 30 white-tailed prairie dog plots and 39 black-tailed prairie dog plots. Using regression models with constants (Biggins and others [1993] reported regression through the origin), the relationships between densities of active burrows and density of prairie dogs as determined by visual counts were highly significant for both species (white-tailed prairie dogs, $F_{1,28} = 86.282$, $P < 0.001$, $R^2 = 0.755$; black-tailed prairie dogs, $F_{1,37} = 29.390$, $P < 0.001$, $R^2 = 0.443$). A comparison of the studies done by Severson and Plumb (1998) and Biggins and others (1993) reveals differences in several key features that collectively may affect the power to detect correlations (table 1). Collectively, the relative ranges of values and various levels of sampling intensity (e.g., plot size, number of plots, geographic coverage) should have given an advantage to the data sets of Biggins and others (1993). Intensity of transect sampling to estimate burrow density is as important as other features but was not reported by Severson and Plumb (1998).

Evidence of the utility of the burrow transect technique is also provided by data generated from its use. The overall collapse of the Meeteetse complex of white-tailed prairie dogs was documented by using densities of active burrows derived from strip transect sampling (fig. 5). It would be difficult to imagine that the downward trend during the 10-year study was an artifact of the sampling procedure, even without the corroborative evidence that exists from visual counts (D.

Table 1. Attributes of two studies on the relationship between densities of black-tailed prairie dogs (*Cynomys ludovicianus*) and densities of their active burrows.

	Severson and Plumb (1989)	Biggins and others (1993)
Number of States	1	3
Number of plots	24	39
Plot size (ha)	4	9
Area sampled (ha)	96	351
Burrow transects (km)	?	248
Lowest prairie dog density (no./ha)	8	0.8
Highest prairie dog density (no./ha)	46	54.2

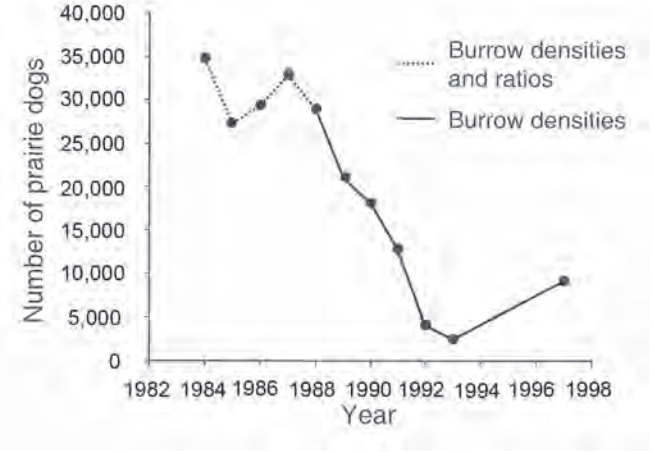


Figure 5. Estimates of white-tailed prairie dogs (*Cynomys leucurus*) on the Meeteetse, Wyo., complex, derived from estimates of active burrow density (Biggins and others, 1993). (Adapted from Biggins and Kosoy, 2001. Reprinted with permission of the *Journal of the Idaho Academy of Science*, Pocatello, Idaho.)

Biggins, unpub. data, 1988–93) that were repeated annually over most of that time period.

The purpose of the foregoing discussion is simply to provide evidence that burrow indices are a useful tool for indexing prairie dog abundance. This does not imply superiority of the technique compared to other tools; methods must be matched to objectives, size of area to be sampled, local conditions, and available funding.

Reemphasizing Percent of a Complex Occupied by Prairie Dog Colonies

Spatial relationships and shapes of prairie dog colonies were discussed above in the context of small islands and peninsulas of habitat with high prairie dog densities. Others (Forrest and others, 1985; Houston and others, 1986; Miller and others, 1988; Biggins and others, 1993) have discussed spatial arrangements of prairie dog colonies at larger scales, implying that some measure of colony arrangement or density within a complex is necessary to adequately evaluate habitat quality for black-footed ferrets. The 7-km limitation to intercolony spacing (Biggins and others, 1993) was a partial solution, but, without additional criteria, vast complexes that are thinly populated with prairie dog colonies may provide the same rating as complexes with more compact arrangements of colonies (fig. 6). There have been theoretical problems with measures of colony dispersion such as intercolony distances (Biggins and others, 1993), ultimately leading the ICC to adopt the conceptually simple tactic of using percent occupied (100 × sum of colony area/total area of complex) proposed by Miller and others (1988). During the first decade of ferret reintroductions, however, the spatial arrangement of prairie dog colonies within complexes largely has been ignored. Few participants have bothered to calculate the percent occupied attribute suggested as an overview of dispersion of colonies. By invoking the new procedure for defining subcomplexes of colonies spaced at 1.5 km or less, the consequences of this oversight are diminished (but not eliminated). It will be possible to examine how much of a complex consists of high-quality “core” subcomplexes. Subcomplexes should be rated separately from 7-km complexes; they should no longer be considered as having equal quality to complexes with the same cumulative area occupied by prairie dog colonies (fig. 6C versus 6A and 6B). Nevertheless, calculation of the proportion of complexes and subcomplexes occupied by prairie dog colonies will provide useful additional information (e.g., to distinguish between complexes such as A and B of fig. 6), and we continue to recommend that management teams at all reintroduction sites make these simple measurements. The technique will allow improved comparisons of complexes and subcomplexes among and within ferret reintroduction sites and may help characterize the potential for colony expansion.

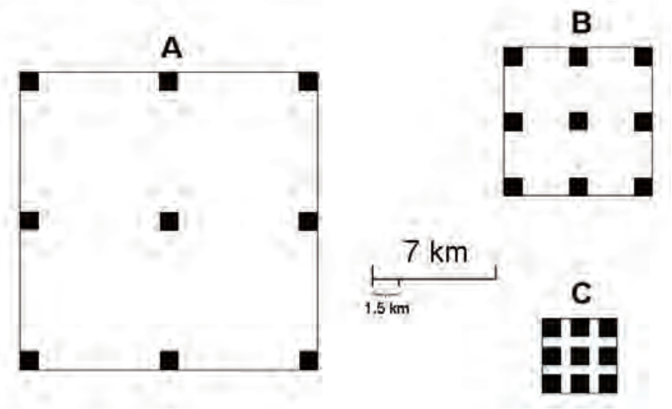


Figure 6. In these three hypothetical complexes, total area occupied by prairie dog (*Cynomys* spp.) colonies (shaded squares) is the same (1,000 ha), but the percentages of each complex occupied by colonies are 4%, 14%, and 57% for A, B, and C, respectively. Are the complexes of equal quality as habitat for black-footed ferrets (*Mustela nigripes*)? Arrangement C qualifies as a subcomplex because of intercolony spacing of <1.5 km.

Summary of the Procedure for Evaluating Ferret Habitat

The following steps for evaluating habitat for black-footed ferrets summarize the approach suggested by Biggins and others (1993) and the modifications presented herein.

1. Map the complex of prairie dog colonies.
2. Circumscribe the complex by using the 7-km criterion.
3. Circumscribe high-quality subcomplexes by using the 1.5-km criterion.
4. Estimate areas of complex, subcomplexes, and colonies with geographic information system (GIS) software if maps are digital. Use polar planimeter or other methods (e.g., dot grid) to estimate areas if only hard copies of maps are available.
5. Calculate percent of complex and subcomplexes occupied by prairie dog colonies.
6. Estimate prairie dog densities on colonies by using burrow density transects or visual counts.
7. Enter density and area estimates for each colony into separate spreadsheets for the overall complex and all subcomplexes.
8. Calculate ferret family ratings by using modified formulae (example spreadsheets with formulae are available from the authors).

Assumptions and Unresolved Questions

We believe that the suggested modifications discussed above will improve the existing model but reiterate that any model is only an approximation of reality (Biggins and others, 1993). Reflection on the basic assumptions involved in this exercise serves as a reminder of its inexact nature. Assumptions include (1) the average prairie dog weighs 760 g, (2) a ferret wastes 20 percent of each prairie dog it kills, (3) the several steps involved in estimating caloric demands of ferrets are correct, (4) losses of prairie dogs to other causes are 250 percent of losses caused by ferret predation, (5) the intrinsic rate of growth for prairie dog populations (λ) is 1.0, and (6) prairie dog populations remain stable. A sobering fact is that some of these attributes vary widely (e.g., numbers 4 and 5) and are in need of further study. The earlier model implicitly assumes that all prairie dogs, regardless of sex or age, are equally available as prey. If female ferrets selectively prey upon juvenile prairie dogs, their own productivity may be more closely correlated with prairie dog productivity than with prairie dog density. This possibility leads to questions about links between forage production, prairie dog production, and ferret production and highlights the potential importance of local and annual variation in precipitation.

A better understanding of prairie dog torpor (Lehmer and Biggins, 2005), burrow-plugging behavior, and energetics of ferret digging behavior could also improve the quality of these models. Is the digging involved in excavating hibernating prey more energetically costly than hunting of nonhibernating prey (Harrington and others, 2003)? What is the balance in tradeoffs between energetic costs of accessing prey and risk of injury in killing prey when comparing hibernating and nonhibernating prairie dogs? Does the presumably lower risk involved in killing hibernating prey allow use of larger prairie dogs that might not otherwise be available?

Territoriality in ferrets also remains poorly understood. Key questions include the following: (1) At what densities of prey does control of minimum space take precedence over control of prey resources? Can our proposed curve be further refined? (2) Does nepotism affect territory size and overlap (i.e., are females more tolerant of their female offspring than of less closely related females)? (3) How do shapes and arrangements of high-quality patches within and among colonies affect territorial behavior?

Some related topics would be appropriate for additional investigation. The earlier attempt to define minimum habitat attributes necessary to sustain female ferret reproduction (Biggins and others, 1993) may be questioned. Further study of female ferret behavior on white-tailed prairie dog or Gunnison's prairie dog (*Cynomys gunnisoni*) colonies, where prey densities are low, would help establish the lower limits. Preliminary data suggest a positive correlation between productivity of female ferrets and density of burrows in the habitat they occupy (D. Biggins, M. Matchett, and T. Livieri, unpub. data, 1997–2000), a relationship that also suggests further research on habitats with low prey densities. Territorial behavior of male ferrets has been ignored but may be an important factor in extinction risk for small populations (Conservation Breeding Specialist Group, 2004). Increasing numbers of black-footed ferrets in reintroduced populations are providing more opportunity to investigate these and other important aspects of ferret ecology.

References Cited

Bevers, M., Hof, J., Uresk, D.W., and Schenbeck, G.L., 1997, Spatial optimization of prairie dog colonies for black-footed ferret recovery: Operations Research, v. 45, p. 495–507.

Biggins, D.E., and Kosoy, M.Y., 2001, Disruptions of ecosystems in western North America due to invasion by plague: Journal of the Idaho Academy of Science, v. 37, p. 62–65.

Biggins, D.E., Miller, B.J., Clark, T.W., and Reading, R.P., 1997, Management of an endangered species—the black-footed ferret, *in* Meffe, G., and Carroll, R., eds., An introduction to conservation biology (2d ed.): Sunderland, Mass., Sinauer Associates, Inc., p. 420–426.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Biggins, D.E., Schroeder, M., Forrest, S., and Richardson, L., 1985, Movements and habitat relationships of radio-tagged black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 11.1–11.17.

Biggins, D.E., Sidle, J.G., Seery, D.B., and Ernst, A.E., 2006, Estimating the abundance of prairie dogs, *in* Hoogland, J.L., ed., Conservation of the black-tailed prairie dog: Washington, D.C., Island Press, p. 94–107.

Campbell, T.M., III, Clark, T.W., Richardson, L., Forrest, S.C., and Houston, B.R., 1987, Food habits of Wyoming black-footed ferrets: American Midland Naturalist, v. 117, p. 208–210.

Clark, T.W., Richardson, L., Forrest, S.C., Campbell, T.M., III, Casey, D., and Fagerstone, K.A., 1985, Black-footed ferret prey base, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 7.1–7.7.

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management planning workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

Forrest, S.C., Clark, T.W., Richardson, L., and Campbell, T.M., III, 1985, Black-footed ferret habitat—some management and reintroduction considerations: Cheyenne, Wyoming BLM Wildlife Technical Bulletin No. 2, 49 p.

Harrington, L.A., Biggins, D.E., and Alldredge, W., 2003, Basal metabolism of the black-footed ferret (*Mustela nigripes*) and the Siberian polecat (*M. eversmannii*): Journal of Mammalogy, v. 84, p. 497–504.

Hillman, C.N., 1968, Field observations of black-footed ferrets in South Dakota: Transactions of the North American Wildlife and Natural Resources Conference, v. 33, p. 433–443.

Hillman, C.N., and Linder, R.L., 1973, The black-footed ferret, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 10–20.

Hillman, C.N., Linder, R.L., and Dahlgren, R.B., 1979, Prairie dog distributions in areas inhabited by black-footed ferrets: American Midland Naturalist, v. 102, p. 185–187.

Houston, B.R., Clark, T.W., and Minta, S., 1986, Habitat suitability index model for the black-footed ferret—a method to locate transplant sites: Great Basin Naturalist Memoirs No. 8, p. 99–114.

Joyce, S.L., 1988, Feeding behavior and water requirements of black-footed ferrets (*Mustela nigripes*): Laramie, University of Wyoming, M.S. thesis, 82 p.

King, C., 1990, The natural history of weasels and stoats: Ithaca, N.Y., Cornell University Press, 253 p.

Lehmer, E.M., and Biggins, D.E., 2005, Variations in torpor patterns of free-ranging black-tailed and Utah prairie dogs across gradients of elevation: Journal of Mammalogy, v. 86, p. 15–21.

Leopold, A., 1933, Game management: New York, Charles Scribner’s Sons, 481 p.

Linder, R.L., Dahlgren, R.B., and Hillman, C.N., 1972, Black-footed ferret–prairie dog interrelationships, *in* Symposium on rare and endangered wildlife of the Southwestern United States: Santa Fe, New Mexico Department of Game and Fish, p. 22–37.

Miller, B.J., Menkens, G.E., and Anderson, S.H., 1988, A field habitat model of black-footed ferrets, *in* Eighth Great Plains Wildlife Damage Control Workshop Proceedings: U.S. Department of Agriculture, Forest Service, General Technical Report RM-154, p. 98–102.

Paunovich, R., and Forrest, S.C., 1987, Activity of a wild black-footed ferret litter: Prairie Naturalist, v. 19, p. 159–162.

Pearl, R., and Reed, L.J., 1920, On the rate of growth of the population of the United States since 1790 and its mathematical representation: Proceedings of the National Academy of Sciences, v. 6, p. 275–288.

Powell, R.A., 1979, Mustelid spacing patterns—variations on a theme by *Mustela*: Zeitschrift für Tierpsychology, v. 50, p. 153–165.

Powell, R.A., Clark, T.W., Richardson, L., and Forrest, S.C., 1985, Black-footed ferret (*Mustela nigripes*) energy expenditure and prey requirements: Biological Conservation, v. 34, p. 1–15.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming (USA): American Midland Naturalist, v. 117, p. 225–239.

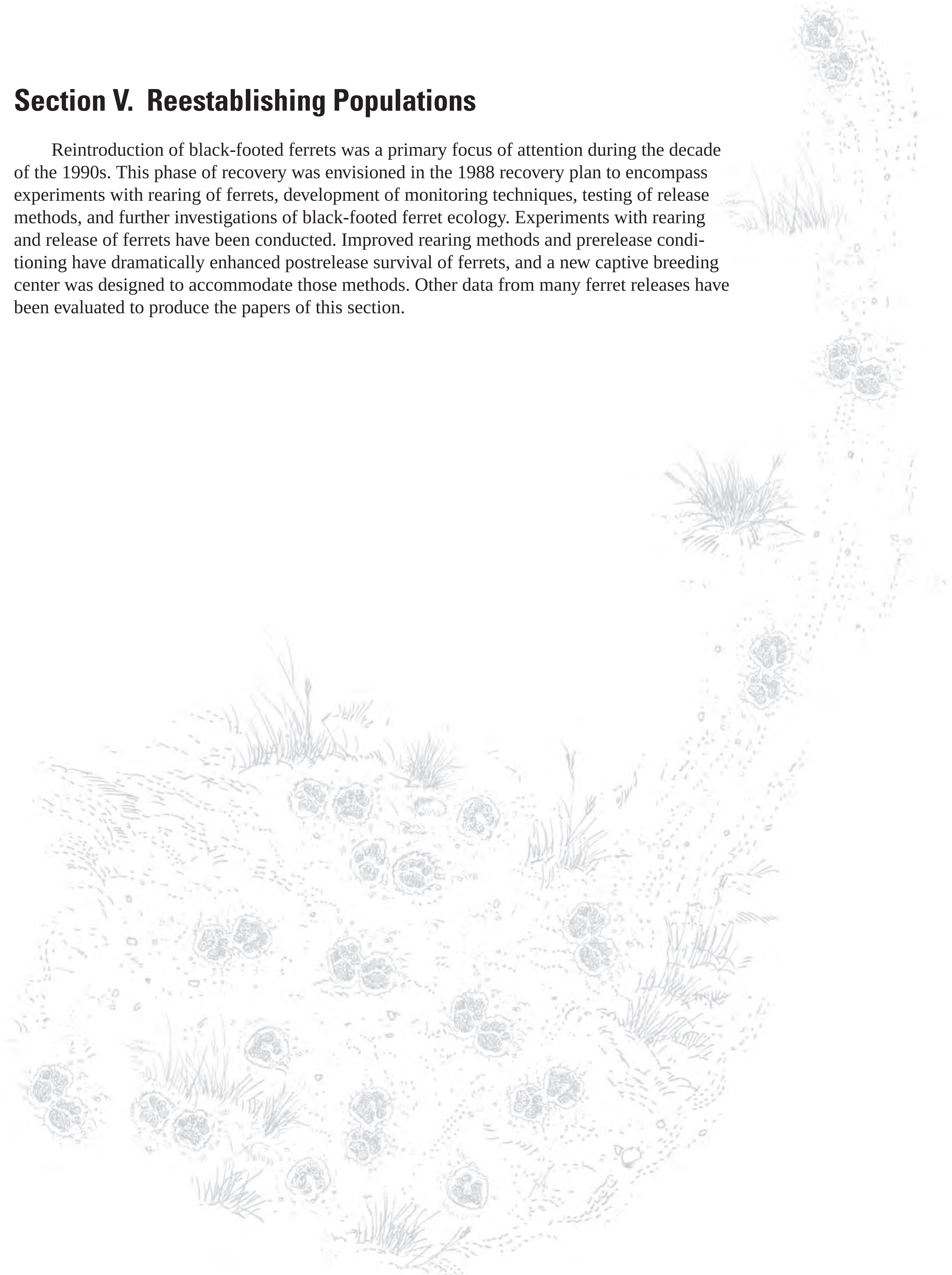
Severson, K.E., and Plumb, G.E., 1998, Comparison of methods to estimate population densities of black-tailed prairie dogs: Wildlife Society Bulletin, v. 26, p. 859–866.

Sheets, R.G., Linder, R.L., and Dahlgren, R.B., 1972, Food habits of two litters of black-footed ferrets in South Dakota: American Midland Naturalist, v. 87, p. 249–251.

Stromberg, M.R., Rayburn, R.L., and Clark, T.W., 1983, Black-footed ferret energy requirements—an energy balance estimate: Journal of Wildlife Management, v. 47, p. 67–73.

Section V. Reestablishing Populations

Reintroduction of black-footed ferrets was a primary focus of attention during the decade of the 1990s. This phase of recovery was envisioned in the 1988 recovery plan to encompass experiments with rearing of ferrets, development of monitoring techniques, testing of release methods, and further investigations of black-footed ferret ecology. Experiments with rearing and release of ferrets have been conducted. Improved rearing methods and prerelease conditioning have dramatically enhanced postrelease survival of ferrets, and a new captive breeding center was designed to accommodate those methods. Other data from many ferret releases have been evaluated to produce the papers of this section.



Monitoring Black-footed Ferrets During Reestablishment of Free-ranging Populations: Discussion of Alternative Methods and Recommended Minimum Standards

By Dean E. Biggins,[1] Jerry L. Godbey,[1] Marc R. Matchett,[2] Louis R. Hanebury,[3] Travis M. Livieri,[4] and Paul E. Marinari[5]

Abstract

Although the monitoring of black-footed ferret (*Mustela nigripes*) populations following reintroductions has not been haphazard, several ferret recovery groups since 1994 have recommended development of uniform standards prescribing minimum methods, intensities, and frequencies of monitoring that would provide data on population size, mortality rates, and recruitment. Such standards would promote comparability of data among sites, document expectations for those who will attempt to establish new populations, and allow the U.S. Fish and Wildlife Service and other responsible groups to better assess progress made toward achieving recovery objectives. Our recommendations are based on methods that have been successfully used to monitor natural and reintroduced populations of ferrets and are an attempt to balance needs and costs. We suggest a combination of marking ferrets with passive integrated transponder (PIT) tags and annual spotlight searches coupled with automated transponder readers to individually identify survivors. Unmarked ferrets should be captured and implanted with PIT tags whenever possible. These and other methods are detailed. Circumstances that may dictate other methods or more intensive monitoring (e.g., high rates of loss or low recruitment) also are discussed.

Keywords: anesthesia, black-footed ferret, monitor, *Mustela nigripes*, snow tracking, spotlight, transponder, trap

Introduction

The need to prescribe standards for monitoring black-footed ferrets (*Mustela nigripes*) at reintroduction sites has become apparent to the U.S. Fish and Wildlife Service (FWS) and members of the Black-footed Ferret Interstate Coordinating Committee (ICC), who discussed formulating standards at the ICC annual meetings of 1994 and 1995. That need was reaffirmed as an action item in an American Zoo and Aquarium Association program review (Hutchins and others, 1996) and at the Black-footed Ferret Conservation Subcommittee (of the Black-footed Ferret Recovery Implementation Team) meeting of 2001. Standards are needed in order to (1) accurately assess progress toward recovery goals, (2) clearly define monitoring expectations for future sites for black-footed ferret reintroduction, (3) provide guidance regarding methods and associated limitations, (4) assure FWS that participants provide consistent feedback on progress, and (5) make limited data comparable for broad-scale interpretations.

The need for standards does not imply that monitoring is presently haphazard. Indeed, several groups releasing black-footed ferrets have used similar strategies, most commonly spotlighting, to evaluate ferret status and trends; however, standardizing would increase the opportunity for comparisons among sites, years, and other variables of interest. Our suggestions are an attempt to balance needs and cost. Our goal was to prescribe methods that maximize applicability of the most basic data but would not preclude any group from participation because of cost. Reviews of monitoring efforts during the early years of ferret reintroductions in Wyoming, Montana, South Dakota, Arizona, Utah, Colorado, and Mexico revealed strengths and weaknesses that influenced our recommendations. This prescription defines minimum levels of monitoring, but we encourage all working groups to consider using more intensive monitoring efforts, when applicable, to help address questions of importance to recovery goals.

We are not suggesting procedures for so-called clearances (U.S. Fish and Wildlife Service, 1988) related to section 7 of the Endangered Species Act, although some of the techniques we discuss are useful for those purposes. We do not exhaustively analyze or describe methods beyond the minimum

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prescription (e.g., radio telemetry) but provide references for more information on those topics. We describe monitoring of black-footed ferrets only; monitoring of prairie dog populations, associated species, and diseases at reintroduction sites is also important, but such topics are beyond the scope of this paper.

Objectives

To monitor is to watch, observe, or check, especially for a real purpose (*Webster's New Collegiate Dictionary*). Monitoring is needed to accomplish the following objectives:

- assess progress toward site-specific population establishment and make attendant decisions related to the need to continue to release captive-bred animals and numbers that should be released,
- detect serious problems or catastrophic population declines (e.g., due to diseases) that might be remediated,
- assess recovery at the national level, and
- test hypotheses regarding methods involved in establishing self-sustaining ferret populations (e.g., rearing, release, translocation, disease prevention, ferret searches, predation reduction).

Specifically, monitoring may provide data to (1) estimate population size, composition, and rates of natality and mortality; (2) assess genetic representation within a population; (3) identify causes of mortality; (4) document spatial distribution of ferrets including dispersal and habitat use; and (5) assess condition of ferrets, exposure to diseases, and parasite loads.

Types of Data: Balancing Needs and Costs

Useful minimum monitoring levels must produce information that identifies whether or not there are serious problems and allows assessment of progress toward local and national recovery goals (the first three objectives listed above). If losses of ferrets are low during initial releases, and if later populations appear to be self-sustaining, then monitoring can be maintained at these minimum levels. If problems are evident (e.g., excessive losses of ferrets), then we suggest increased levels of monitoring to identify their causes. The alternatives are site abandonment or sustained augmentation of ferrets. Abandonment does not contribute to our understanding and may result in repeated mistakes. Sustained augmentation seems inefficient but may, in the end, be needed at some sites.

The fourth listed objective of monitoring relates to experimentation and hypothesis testing to better understand the ecology of ferrets and improve reintroduction strategies, thereby enhancing the prospect for successful species recovery. This objective may necessitate monitoring that is different and sometimes more intensive than the minimum levels prescribed below. This learning objective is sufficiently important to programmatic decisions that it may at times take precedence over other objectives. Needs vary by site and year; further discussion of this objective is beyond the scope of this paper.

Minimum data needed to accomplish the first three objectives are estimates of population size, survival rates, and annual recruitment. A critical review of the last four decades of black-footed ferret monitoring, however, reveals that there never have been estimates of these attributes that were free of known biases. Recently, we have qualified these estimates as “minimums,” recognizing that not all ferrets will be found (Biggins and others, 1998). Moreover, “survival” rates should really be termed “retention” rates, where failure to retain ferrets at a reintroduction site can be due to emigration or mortality. Retention rates are likely biased downward because of undetected ferrets, but actual survival rates could be higher than retention rates if dispersal away from the reintroduction sites occurred without concurrent mortality. Population size, survival, recruitment, and associated variances can be estimated with closed form models or iterative numerical optimization if unbiased surveys are repeated over short time spans (Otis and others, 1978; White and others, 1982), and even more analytical tools are available if those multiple surveys done in short spans are replicated again over longer spans (robust designs: Kendall and others, 1995; Hines and others, 2003; program MARK: White and Burnham, 1999). The increased effort in repeated surveys is obvious, but avoiding bias caused by observer familiarity gained during previous surveys calls for additional constraints, problematic logistics, and even greater costs. Thus, we believe that the effort required could not be sustained over multiple reintroduction sites and years; the 24-year history of rather intensive monitoring of black-footed ferrets provides ample evidence regarding how much can be accomplished with available resources. Realistically, the tactics that have been used over the past 10 years are likely to remain the ones used to monitor black-footed ferret populations in the future, and the measures of population size, survival, and recruitment obtained by those monitoring methods (described below) will have to serve as indices to population attributes.

Although those indices (e.g., population size) are biased, they are nearly always based on complete coverage of respective reintroduction sites during spotlight surveys. Thus, issues of spatial sampling are not relevant. Although coverage may be complete, the counts are not a census because all ferrets are not found. We do not regard this bias as a fatal flaw, in part because it is unlikely to be large and in part because the counts can be adjusted for effort, providing indices that are particularly useful in a comparative sense (e.g., comparisons among groups and years within sites). Diminishing cumulative detections of unique ferrets over several days of spotlight searches (discussed below) provide reassuring evidence that large numbers of ferrets usually do not remain undetected during spotlight surveys. The standardization of search methods suggested below also will enhance comparability of data sets.

Data Collection Methods

Relatively few techniques have proven effective to “watch, observe, and check” black-footed ferrets; each method has its advantages, disadvantages, limitations, and risks. The methods currently used are snow tracking, spotlighting, capture-mark-recapture, and radio telemetry, but each can be utilized at varying levels of intensity and can be coupled with other strategies to increase the quality and quantity of data. Indeed, use of multiple methods allows cross-checking and verification of data.

Snow Tracking

Snow tracking involves searching from the ground or aircraft to locate tracks and other sign (especially diggings) of black-footed ferrets. Individual ferrets can sometimes be identified based on geographic location of tracks and origin and terminus points. Counts can be cumulative, giving an estimate of ferret numbers, provided that snow conditions remain optimal for at least several days. The strategy involves searching along ground transects (Richardson and others, 1987) or aerial flight lines (Biggins and Engeman, 1986; Miller and Biggins, 1988) until tracks or diggings are encountered. Track sets then are individually followed from origin to terminus to determine individuality and gather accessory information on movement pattern (use of space, but only crudely related to time) and to opportunistically collect scat for diet information. Broad-scale searches for tracks have revealed the presence of ferrets on prairie dog colonies that would not otherwise have been monitored. Absence of tracks, however, does not prove absence of ferrets because ferrets may remain inactive for many days following a snowstorm.

Snow tracking is least likely to adversely impact ferrets, requires little specialized equipment, and is relatively inexpensive. The principal disadvantage is weather dependency; although snow is common in the northern and western portion of the ferret’s original range, good tracking conditions occur only sporadically. Best results are attained when snow cover is continuous and undisturbed for several days. Warm sunny spells can cause patchiness, and winds can quickly erase evidence. Prairie dog (*Cynomys* spp.) tracks cause confusion during searches from the air and ground and may obliterate ferret tracks; however, white-tailed prairie dogs (*C. leucurus*) and Gunnison’s prairie dogs (*C. gunnisoni*) routinely hibernate, and black-tailed prairie dogs (*C. ludovicianus*) also may enter torpor (Lehmer and others, 2001), allowing effective midwinter ferret searches during prolonged spells of calm, cold weather following accumulations of snow. A team of searchers must respond immediately when favorable conditions develop. Each site should have a snow-tracking plan targeting priority areas for searches so that implementation can be rapid and efficient. Identification of mustelid tracks is not always straightforward; long-tailed weasel (*Mustela frenata*) tracks cause potential confusion (Miller and Biggins, 1988). Individual identities of ferrets can be ascertained if they have been marked with passive integrated transponder (PIT) tags (see subsection on Capture, Handling, and Marking). If ferrets are not individually identified, conservative time and space separation criteria should be used (see subsection on Minimum Level of Monitoring) to determine the minimum number of different ferrets present because ferrets can move long distances each night and because several ferrets can reside in close proximity.

Spotlighting

Spotlighting has been the universal technique for finding black-footed ferrets (Campbell and others, 1985). Prairie dog colonies are scanned at night with high-intensity spotlights by individuals on foot or in vehicles (e.g., all-terrain vehicles or trucks). Recently, most spotlighting has been conducted by using continuous illumination while the observer moves slowly (10 km/h), but earlier workers, searching on relatively small prairie dog colonies, preferred a systematic schedule of intermittent illumination from a fixed location (Henderson and others, 1969; Fortenbery, 1972). Standardization to the extent possible is very important because variation in the manner of implementation can lead to erratic results, but standardization must be balanced with site-specific needs.

Compared to snow tracking, spotlighting gives much more accurate temporal data to accompany spatial data. The eyes of ferrets reflect an emerald green shine, but other animals, such as badgers (*Taxidea taxus*), coyotes (*Canis latrans*), weasels (*Mustela* spp.), deer (*Odocoileus* spp.), and pronghorns (*Antilocapra americana*), can cause confusion. Interorbital distance, distance from ground, and behaviors help distinguish ferrets from some other mammals, but distances can be deceiving at night, and experience is necessary for reliable and efficient identification. Coyotes tend to briefly look at the spotlight, run a short distance, stop, and then look at the spotlight again. Weasels dart about much more quickly than ferrets and have a more subdued eyeshine. Swift foxes (*Vulpes velox*) run with a rigid gait, so the eyeshine does not undulate, then may stop and briefly lay close to the ground. When ferrets are moving, their eyeshine tends to bounce because of their bounding gait. Deer and pronghorns have much larger eyes and tend to be bedded down at night in groups; their eyeshine rises when they stand up.

Reported detection rates range from 1.4–102.6 hours per black-footed ferret sighting and up to nearly 264 hours per unique ferret located (table 1) for surveys of reintroduced and wild populations. Sighting rates are influenced by ferret density, but topography, vegetation, and varying behaviors of the animals (e.g., because of weather, season, origin of stock, rearing method) may also contribute to variation in sightability

Table 1. Examples of search efforts expended for locating black-footed ferrets (*Mustela nigripes*) with spotlights.

Location	Time	Source	Hours	Number of hours/ ferret sighting	Number of hours/unique ferret sighting
Southwest South Dakota	1966–67	Hillman (1968)	462.0	4.0	
Meeteetse, Wyo.	Summer 1983	Forrest and others (1988)	260.0		3.0
	Summer 1984	Forrest and others (1988)	554.0		4.3
	Summer 1985	Forrest and others (1988)	647.0		11.2
Shirley Basin, Wyo.	October 1991	Hnilicka and Luce (1992)	121.5		12.2
	November 1991	Hnilicka and Luce (1992)	258.5		28.7
	Summer 1992	Hnilicka and Luce (1993)	1,256.1	35.9	125.6
	November 1992	Hnilicka and Luce (1993)	925.1	17.5	51.4
	Summer 1993	Luce and others (1994)	675.8		35.6
	October 1993	Luce and others (1994)	1,244.7		52.0
	Summer 1994	Staley and Luce (1995)	570.7		95.1
	October 1994	Staley and Luce (1995)	591.3	34.8	118.3
C.M. Russell NWR, Mont.	1994–96	Stoneberg (1996)	952.7	3.1	5.9
Conata Basin/Badlands, S. Dak.	Fall 1994	Plumb and Marinari (1996)	247.5	7.7	35.4
	Summer 1995	Plumb and Marinari (1996)	600.4	26.1	66.7
Conata Basin, S. Dak.	September 16–23, 2002	T. Livieri (unpub. data)	462.0	1.4	3.1
Aubrey Valley, Ariz.	June–December 2002	Winstead and others (2003)	1,847.0	102.6	263.9
Aubrey Valley, Ariz.	June–November 2003	Hoss and others (2004)	2,014.0	69.4	83.9

(Marinari, 1992). The probability of detecting an individual free-ranging ferret with spotlights has not been estimated for any set of conditions. Cumulative counts over time, however, have been plotted and may generically illustrate probability of detection during short time spans, assuming no mortality occurs. Data from the Meeteetse, Wyo., population of ferrets on white-tailed prairie dog habitat suggest that about 82 percent of the cumulative total number of ferrets had been counted after four nights of spotlight searches (Forrest and others, 1988). Similar data from spotlighting in 17 black-tailed prairie dog colonies in the Conata Basin of South Dakota (T. Livieri, unpub. data, 2002) resulted in a steeper curve, with 92 percent of the cumulative total counted after three nights and 98.5 percent counted after four nights (fig. 1). For the South Dakota data set, the cumulative proportion of ferrets counted also increased as a function of cumulative time spent spotlighting adjusted by area covered during the search (fig. 2). Although most ferrets appear to be found during diligent searches, individuals can be elusive. In Utah, a female remained undetected for 24 months (three surveys) (B. Zwetzig, oral commun., 2004); in Arizona, two females were not located for 27 months (Hoss and others, 2004); and an adult male in South Dakota was first relocated 40 months after release (W. Perry, oral commun., 1998).

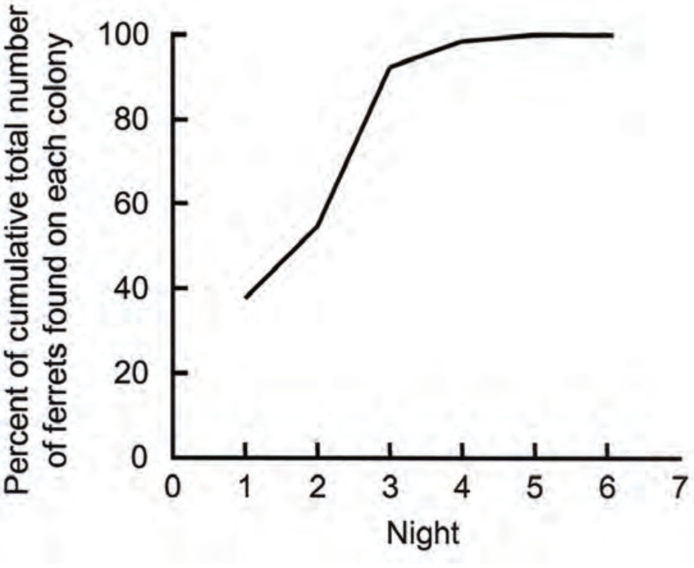

Figure 1. Black-footed ferrets (*Mustela nigripes*) encountered per night during spotlight searches on 17 black-tailed prairie dog (*Cynomys ludovicianus*) colonies, September 16-22, 2002, in Conata Basin, S. Dak.

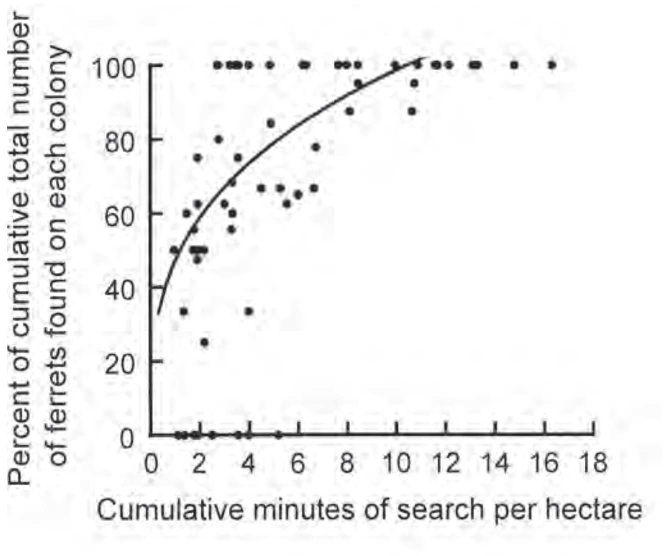

Figure 2. Black-footed ferrets (*Mustela nigripes*) encountered per minute per hectare during spotlight searches on 17 black-tailed prairie dog (*Cynomys ludovicianus*) colonies, September 16-22, 2002, in Conata Basin, S. Dak. An exponential curve was fitted to data.

Table 2. Percent of the cumulative total number of black-footed ferrets (*Mustela nigripes*) counted during 1999–2002 at Conata Basin, S. Dak.

	Cumulative counts				
	1999	2000	2001	2002	Mean
			Males		
July–August	71.4	70.0	85.2	65.4	73.0
September	92.9	76.7	92.6	96.2	89.6
October	92.9	93.3	100.0	100.0	96.6
November	100.0	96.7	100.0	100.0	99.2
December–on	100.0	100.0	100.0	100.0	100.0
			Females		
July–August	93.9	92.9	88.3	94.1	92.3
September	100.0	100.0	95.0	100.0	98.8
October	100.0	100.0	100.0	100.0	100.0
November	100.0	100.0	100.0	100.0	100.0
December–on	100.0	100.0	100.0	100.0	100.0

Cumulative total spotlight counts of ferrets continue to increase over time spans of months, but in these longer spans it is not reasonable to assume that the estimates are unaffected by losses of animals. For a 4-year data set from South Dakota (T. Livieri, unpub. data, 1999–2002; data from those colonies that were repeatedly searched each month), monthly detection rates for males appeared to be lower than rates for females (table 2). Assuming a constant monthly survival rate of 0.9763 (annual survival of 75 percent), the increasing cumulative monthly counts in table 2 can be approximated by (constant) monthly spotlight detection rates of 0.722 for males and 0.918 for females. These estimates need refinement but seem to reflect differences in ability to detect adult males and adult females with spotlight searches.

Spotlighting can alter behaviors of black-footed ferrets. Responses to the lights seem to vary among individual ferrets. Some ferrets may avoid the light by decreasing aboveground activity, and others may attempt to escape through increased movements (Campbell and others, 1985). Spotlights emitting white light probably should not be used for prolonged observations of a ferret (Campbell and others, 1985). More equipment (e.g., spotlights, backpack units, batteries) is needed for spotlighting than for snow tracking. Similar to snow tracking, located ferrets can be identified with remote transponder readers or through capture.

Capture, Handling, and Marking

Whether ferrets are located by spotlighting or snow tracking, identification of each individual may enable (1) cumulative minimum counts of animals while positively avoiding double counting, (2) an overview of dispersal movements, (3) tests of hypotheses regarding comparisons between treatments (e.g., rearing conditions, sex, site, habitat use, release method; Biggins and others, 1998), and (4) assessment of likely matrilineal relationships within populations (Biggins and Godbey, 2003). With some monitoring designs, marking also may allow (1) use of mark-recapture methods for population estimation (Otis and others, 1978; White and others, 1982; White and Burnham, 1999; Rivest and Daigle, 2004), (2) use of survival estimators (Lebreton and others, 1992), and (3) estimation of age-specific mortality rates.

Successful methods for marking ferrets are passive integrated transponder (PIT) implants (Fagerstone and Johns, 1987) and ear tattoos (Fagerstone and others, 1985). Tattoos are usually identifiable only on ferrets that are in hand and sometimes become illegible or disappear entirely. Less commonly, transponders have ceased functioning or have been lost from the ferrets. Passive integrated transponder tags are relatively inexpensive and easy to install and have become the preferred technique for marking ferrets. Two transponders should be implanted, one on the posterior part of the head and the second dorsally between the hips. After a ferret has been located by spotlighting or snow tracking, its transponders can be identified with an automated reader that is left at the occupied burrow (Stoneberg, 1996) (fig. 3), or the ferret can be captured and identified with a hand-held reader.

If an attempt at automated transponder reading fails, capture can be used as a backup. Capture involves additional stress on animals (Thorne and others, 1985) but provides an

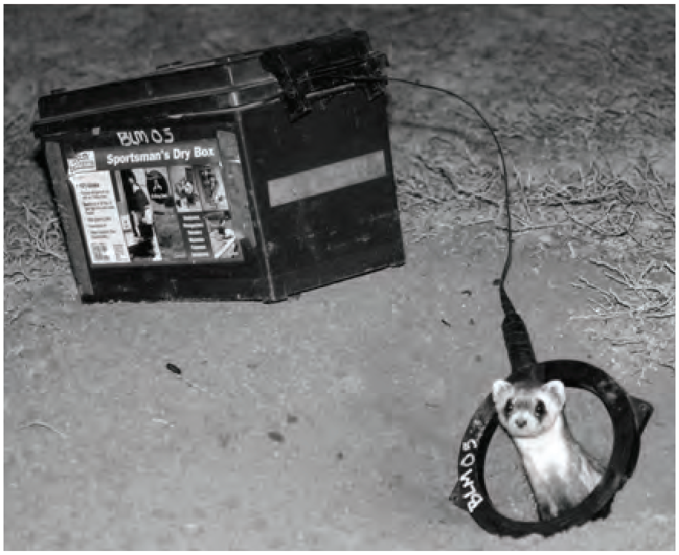

Figure 3. Automated passive integrated transponder readers in waterproof boxes may be left at burrows occupied by black-footed ferrets (*Mustela nigripes*). Transponder numbers will be recorded as the ferret passes near (or through) the loop antenna placed to encircle the burrow entrance.

opportunity to assess condition and take samples of blood, parasites, etc. These samples could prove invaluable in disease evaluations and for genetic studies. Traps (see fig. A1 in appendix) must be in good working order. It is exasperating to find a malfunctioning trap at the end of an extended attempt to capture an animal. If a burrow system is thought to have multiple openings, openings lacking traps may be plugged with rocks, wood, or plastic cups (44 oz). When trapping is finished, all traps must be retrieved, and all burrows must be unplugged.

Dye marking captured ferrets can prevent double counting during a survey and helps identify ferrets already captured during a trapping session. Dye can be applied to captured animals without use of anesthetics. Effective dyes include Nyanzol D (Hoogland, 1995) and hair dyes. Dyes, however, are temporary compared to transponders, lasting at best until the next molt; PIT tags should be used whenever possible, whether or not fur is dyed.

Anesthesia is necessary for many of the procedures mentioned above. Anesthetics used in the field on black-footed ferrets have included ketamine, a ketamine-medetomidine mixture (reversed with atipamezole) (Kreeger and others, 1998), telazol, and isoflurane. Gas anesthesia (including isoflurane) requires a relatively bulky and complicated apparatus, including an induction chamber, vaporizer, mask, oxygen bottle, and connecting tubes. Isoflurane, however, allows a highly controllable level of anesthesia and maintenance of much higher blood oxygen concentrations (Gaynor and others, 1997).

Field technicians who need to capture and handle black-footed ferrets must complete a certification course. Presence of a veterinarian is beneficial when using anesthetics and handling ferrets. Ferrets should not be released until fully recovered from anesthesia, which may take hours with some injectable anesthetics.

Radio Telemetry

Radio telemetry has been used on black-footed ferrets since 1981 (Biggins and others, 1985, 1986). Telemetry has distinct advantages; animals are individually identifiable from remote locations with minimal human disturbance, behaviors can be monitored remotely (e.g., movements, home ranges, activity cycles, dispersal), fates can be identified, additional methods of survival analysis are available (Heisey and Fuller, 1985; Pollock and others, 1989), causes of mortality can be identified, and habitat use can be objectively assessed (White and Garrott, 1990). Disadvantages include the expense and impact of placing transmitter packages on or in the animals. Ferrets are assumed to be influenced by a transmitter, whether external or implanted; the effect can vary from trivial to devastating. Discussions about whether or not to use radio telemetry should focus on the degree of suspected impact weighed against potential gains in knowledge. Neck abrasions have been caused by collars, and premature collar loss has been common. The currently recommended collar is made of wool and degrades within several weeks to months (Biggins, Godbey, Miller, and Hanebury, this volume).

Compared to spotlighting and snow tracking, radio telemetry on black-footed ferrets is expensive and relatively difficult to master. Use of radio triangulation during ferret reintroductions has concentrated on intensive but short-term (30–60 days postrelease) data collection to compare behaviors of animals and document their fates (Biggins and others, 1999: Biggins, Godbey, Livieri, and others, this volume). Less labor-intensive, automated signal detection was used in releases of ferrets in South Dakota and Montana with emphasis on determining fates of ferrets, but interpretation of data was problematic. Because of the large commitment of time and funds and the possibility of adverse impacts on ferrets carrying transmitters, we regard radio telemetry as a specialized tool that should not be considered for routine monitoring of black-footed ferrets (Biggins, Godbey, Miller, and Hanebury, this volume).

Alternative Techniques

Other techniques that have been used in attempts to locate ferrets include scent dogs (Reindl, 2004); scent attractants coupled with remote cameras or transponder readers; implantable radio transmitters; long-range transponders; night vision equipment, such as light amplifiers and infrared detectors; and track plates. To date, these techniques have not proved widely applicable under field conditions, but they may become more useful in the future.

Recommended Standards

Minimum Level of Monitoring

Under the present circumstances and state of technology, we recommend marking all ferrets, including as many wild-born individuals as possible, with two transponder chips; spotlighting to locate black-footed ferrets; and identifying all ferrets located by using combinations of remote transponder readers and capture. Dye marking in addition to PIT tagging can allow the searchers to bypass ferrets, avoiding the need to set a reader or capture the animals to find out if they have already been PIT tagged. Failure to read the PIT tag each time a ferret is located, however, may preclude more rigorous assessments of population attributes and ferret movements. Exactly how these tools are deployed depends on the phase of reintroduction and the objectives for monitoring.

For sites where ferrets are released in fall, we recommend a minimum of two spotlighting periods, the first beginning 30 days after the final release (if there were several, closely spaced, sequential releases) and the second, postreproductive survey beginning in August of the following year. An existing ferret population that has not received additional releases of ferrets during the previous 12 months may be monitored with an August survey only. A prebreeding survey in March–April is highly desirable (for both recently released and established populations) but is not considered a requirement. If possible, ferret searches should be conducted during bright moonlight. Preliminary analyses for Siberian polecats (*M. eversmannii*) and black-footed ferrets suggest that radio-tagged individuals of both species were more active during bright nights (full moon) than during dark nights (new moon); when the moon was partially illuminated, they were more active during the part of the night when moonlight was present than when it was absent (Biggins, 2000).

Clark and others (1984) suggested methods for locating ferrets, and the FWS later recommended criteria for black-footed ferret surveys to clear prairie dog towns for development activities, application of toxicants, or other actions that might be detrimental to an existing population of black-footed ferrets (U.S. Fish and Wildlife Service, 1988). Because the guidelines were developed from techniques used at Meeteetse to monitor a wild population, some aspects are applicable to the standards proposed here for monitoring released ferrets. The basic recommendations of the survey guidelines are reiterated below, and each of these is followed by suggested modifications (if any) applicable to the minimum standards for monitoring reintroduced ferret populations.

1. When monitoring existing populations, surveys should be conducted between August 1 and September 30. This is the period when young ferrets have become sufficiently active above ground that they can be captured for marking, and it is normally prior to dispersal so that litters are usually separately identifiable. Adult males seem to be less detectable than adult females during this period (table 2).

2. Prairie dog towns should be continuously surveyed between dusk and dawn on each of three to five consecutive nights to ensure systematic coverage and increased opportunity to discover black-footed ferrets. A ferret can stay inactive for days (Biggins and others, 1986; Richardson and others, 1987), presumably depending on weather and its food supply. We suggest adding more nights (if necessary) until no (or few) new ferrets are found. If scheduling dictates that spotlighting cannot be continuous from dusk until dawn, then gaps in coverage should be rotated among nights so that no time period is neglected.

3. Detection depends on the ferret being above ground and facing the observer at the time the spotlight is directed toward it. Pass the spotlight across the landscape, and follow with a sweep back across the same path. A ferret looking away from the light during the first pass may become curious and turn toward the light on the second pass. Large prairie dog towns should be divided into tracts, and each tract should be systematically and repeatedly searched. Each searcher should concentrate on an area that ensures at least one pass every 30–60 minutes. Rough terrain, dense vegetation, and lack of road access may dictate small tracts to result in effective coverage. On occasion, the objective may be only to document presence or absence of ferrets on colonies, in which case tracts could be large (up to 800 ha). The area should be as small as practical to increase the opportunity for detection. In some cases backpack spotlighting may be necessary (e.g., if vehicle access is impossible or legally restricted). If searches are done on foot, then each person should concentrate on about 130 ha or less. Boundaries of tracts should be well marked to keep searchers oriented at night.

4. Observations on each prairie dog town or tract searched should begin at a different geographic point on each successive night to maximize the chance of intercepting a black-footed ferret during its nighttime activities, the patterns of which tend to be somewhat animal specific and repetitive. Even within a night, searchers should consider varying their search patterns while ensuring even coverage (e.g., alternate traveling north-south and east-west).

5. Previous guidelines suggested that survey crews consist of one vehicle and two observers equipped with two spotlights of 200,000–300,000 candle power. Teams searching for ferrets in areas with known populations have used a wider variety of equipment and organizational strategies. Single searchers on foot, in trucks, and with all-terrain vehicles (ATVs) have been effective, and other types of spotlight equipment also have been used. Because relative efficiency of various strategies is somewhat site dependent, we propose no limits. Use equipment that is suitable for the weather, terrain, and personnel.

Additional specifications include the following:

1. It is better to search each site entirely within a short time span by using a large number of searchers than to use few people over a long time span. The long-span, low-intensity method leads to problems in specifying the time interval for which the estimate is relevant (e.g., for estimating survival) and increases potential for confusion in counting individuals that are not recaptured or otherwise identified (e.g., double counting or missing ferrets that moved).

2. Use a systematic sampling scheme giving uniform coverage to the entire area, even though higher densities of burrows may be present in some areas than others. Resist the temptation to repeatedly return to places where ferrets have been seen. Some of the fringe areas of prairie dog colonies may have the largest populations of prairie dogs, and intuitive perceptions of habitat quality are not always reliable. Provide markers to assist with relocating ferrets and orienting the surveyor.

3. Diligently attempt to identify all ferrets. If a transponder cannot be read remotely, then try to capture the ferret. If some members of the team are more adept at capture than others, then consider using them as a dedicated “capture” crew whose job is to capture and identify ferrets rather than search for them. Occasionally, individual ferrets can be identified by unique physical characteristics that can be distinguished after capture or, even more uncommonly, without capture. Acceptable examples we have seen include deep scars, missing portions of ears, and missing toes. We do not consider differences in coloration and individual mask patterns to be sufficiently reliable for individual identification.

4. If individual ferrets are not identifiable, then we recommend a conservative approach to classifying them as separate individuals. Unless snow allows absolute separation of track sets, ferrets can be classified as separate individuals only if it was nearly impossible for an animal to have moved between the two locations during the time interval between sightings. For sightings separated by <500 m, the sightings must be simultaneous (fig. 4). For sightings separated by longer distances, we assumed a maximum speed of 6 km/h for a ferret, decreasing in a nonlinear manner with increasing distance. This maximum has been used to screen radio-telemetry data for errors (Breck and Biggins, 1997). We reduced the maximum speed to a low of 0.694 km/h with a separation of 50 km because the maximum documented movement of a ferret in a 3-day period was about 50 km (Biggins and others, 1999). Two sightings with distance and time separations that plot above the curves of figure 4 can be assumed to be separate individuals. This approach mandates substantial evidence for inclusion of animals into a population count. To avoid underestimation of population size for unmarked populations, a larger survey crew will be

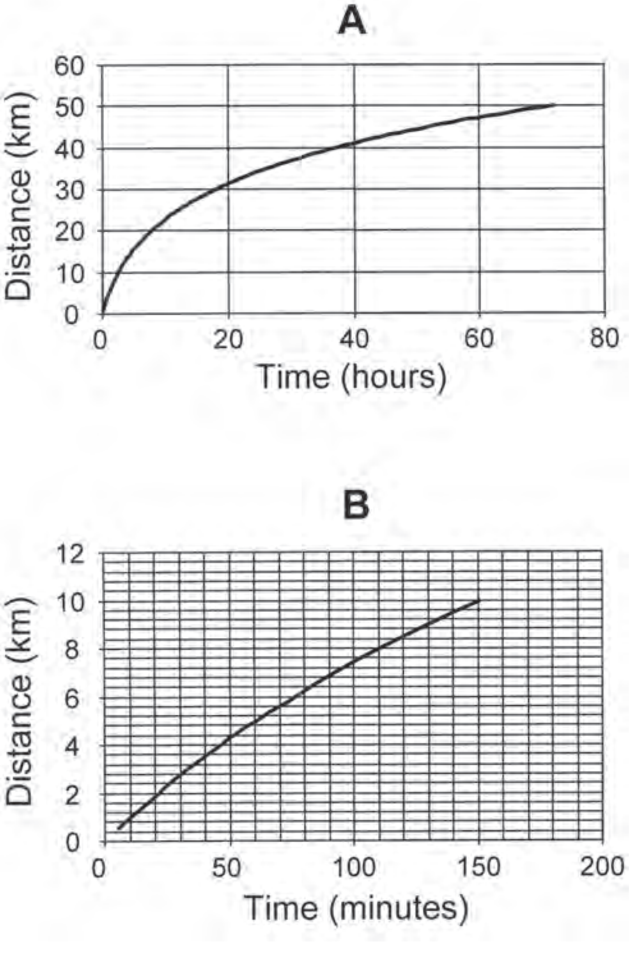

Figure 4. Minimum separations of distance and time needed to classify two sightings of black-footed ferrets (*Mustela nigripes*) as different individuals. Plot B is the lower portion of the curve in plot A, rescaled to provide better resolution. Separations of two sightings plotting above the curves can be considered separate individuals (e.g., two sightings 4 km apart separated by 30 minutes).

necessary (to increase the probability of simultaneous sightings of ferrets living in close proximity to each other).

5. A brief meeting should occur the morning following each spotlight search session to discuss results from the previous night. One important purpose is to assess the number of unique individuals that are likely represented by ferrets seen but not identified (using the criteria of 4 immediately above).

6. Use a standardized form with a map on the reverse side. Record all nonspotlighting periods (e.g., rest breaks) on the form, sketch ferret locations on the map, and place a marked flag at each ferret location. Use Global Positioning System (GPS) equipment to obtain coordinates of ferret locations, and record these coordinates on the data form (see appendix for examples of forms and checklists). Once coordinates and other necessary data have been collected, remove all flags.

7. Ferrets should be double marked before release with two PIT tags (anterior and posterior). At present, incompatibility among manufacturers requires that the ferret program adopt a single system. The tags and readers currently used in the ferret program are made by AVID® Microchip I.D. Systems (Folsom, La.). Transponder technology is developing rapidly, and other systems may be practical in the future.

8. Unmarked ferrets that are wild caught should be marked or re-marked if they have lost previous markings. Field anesthesia by a veterinarian or certified individual is necessary.

9. An annual report to the FWS should include a table listing all ferrets identified in monitoring surveys. Ideally, the table should be in a commonly used computer spreadsheet. For each ferret, the following accessory information should be provided:
   a. Studbook number and field identification number (telemetry number, site-specific wild-born animal number, PIT tag number, etc.)
   b. Sex
   c. Method of identification
   d. Date(s) of capture or identification
   e. Location(s) of capture or identification (Universal Transverse Mercator [UTM] coordinates from GPS receiver; include datum and grid zone)
   f. Observer(s)
   g. Date of original release (if applicable)
   h. Specimens taken (blood, fecal, parasites, etc.)
   i. Other data taken (weight, measurements, etc.)
   j. If previously unmarked wild-born kit, identify litter size and associated dam.

10. A standard release form (see appendix), filled out for each ferret released, should also be forwarded to the Black-footed Ferret Recovery Program Coordinator. As in 9 above, the forms can be tabulated and forwarded in spreadsheet form on a magnetic disk (see Plumb and Marinari [1996] for an example table).

Recommended Precautions—Legality, Human Safety, and Animal Safety

1. If using all-terrain vehicles (ATVs), heavy batteries used to power spotlights can change weight distribution and make the vehicles unstable.

2. Riders of ATVs should be certified if required by the employer. Night operation and use of a spotlight increase the difficulty. Special training should be provided on ATV safety and night use. Use appropriate protective gear and clothing.

3. Obtain all permits and notify appropriate authorities regarding timing and location of spotlighting activity. Spotlighting is prohibited or regulated in some States. A Federal endangered species permit will be required.

4. Listen to weather reports and be familiar with local conditions. Weather can change rapidly, and impending changes may not be obvious at night. Hazards include lightning, dangerously large hail, tornadoes, and disorientation at night, especially in snowstorms. These phenomena are not imaginary; spotlight searchers have had close calls with all of them.

5. Searchers should be fully familiar with their assigned areas, which may require a visit during daylight. A compass or personal GPS unit may allow a technician to avoid becoming lost during thick fog or heavy snowfall. Searchers should work in pairs when there is a threat of adverse weather.

6. The survey crew should be as well equipped as possible with two-way radios. For safety and efficiency, it is especially important to maintain frequent communication with individuals working in remote areas.

7. Landowners must agree (preferably in writing) to the activities being conducted on or around their properties and should be kept well informed of progress.

8. Respect property, whether public or private. Avoid rutting muddy roads, and follow applicable rules and procedures for off-road driving with ATVs or larger vehicles. If you inadvertently damage property (e.g., gates, fences, cattle guards), make any needed repairs or arrange to have them done.

9. Spotlights are disruptive, so minimize the observation time with intense white light. After locating a ferret, it should be observed in the periphery of the light beam, using the least illumination possible to maintain contact for necessary follow-up activities (e.g., transponder reading, trapping). Avoid repeated harassment of the same animal.

10. When trapping, do not separate a mother from her kits for extended periods. Although unusual circumstances may dictate either more lenient or more restrictive limits, we suggest limiting such separations to <24 hours during late July–September. Separations should be much shorter if it becomes necessary to trap an adult female (that has young kits) earlier in the season. Remember that a burrow blocked by a trap can separate the dam from her kits even if no ferrets are caught. Traps should be checked at least once per hour by approaching the trap and looking all the way into it. Closed traps should not be left in burrows (ferrets have been inadvertently caught in closed traps). Badgers and other predators can kill an entrapped ferret, and severe weather can cause hyperthermia or hypothermia.

11. Use properly maintained traps. Traps that are poorly maintained or misused have injured ferrets. For example, ferrets have received abrasions and lacerations when forcing their way through gaps at the back door, even though the doors were secured with clips. We recommend clipping or otherwise fastening each corner of the back door. Check for treadle sensitivity, protruding wires, broken welds, and bent parts. Poorly maintained traps may increase the amount of time spent harassing an animal if repeated attempts become necessary to catch it. Wrapping traps in pieces of wool blanket or burlap helps protect a captured ferret from wind and cold and seems to create a more enticing tunnel that may facilitate capture and keep the animal calm after capture.

12. Ferrets usually should be released into the burrow where they were captured and during hours of darkness whenever possible. If necessary, a ferret may be held in a cool location until the following night. A portion of a prairie dog can be given to any ferret that must be captured for handling or marking to help mitigate the stress of the procedure. If presented at the time of release, ferrets often will take these offerings into the burrow. Prairie dog remains may attract badgers or other predators, so their use should be judicious and closely monitored. If your site is within the known range of plague, we suggest precautions to avoid inadvertently feeding plague-contaminated carcasses (use prairie dogs from plague-free zones or those that have been properly quarantined).

13. Contact the Black-footed Ferret Recovery Program Coordinator for latest developments regarding trapping and handling ferrets, and refer to Thorne and others (1985) for additional details.

The best training for monitoring black-footed ferrets is assisting in an effort that is already underway. Persons who will be responsible for monitoring at a new reintroduction site should participate in monitoring at an existing site well before the new project begins.

Expanding Beyond the Minimum Standards

1. Groups of ferrets may be released sequentially at a site throughout extended periods (60 days or more). Spotlight surveys have been conducted 30 days after the last release (Montana and South Dakota) and 30 days after the midpoint of extended releases (Wyoming). For releases over relatively long spans of time, a solution might be to conduct more than 1 survey at about 30 days postrelease, treating groups of animals as separate releases.

2. Prior estimates of survival of released ferrets using spotlighting data were treated as minimum survival because ferrets may have remained undetected during surveys. With several searches repeated over a short time span (e.g., 2 weeks) true survival rate or population size may be estimable. Separate estimates of the probability of detection and accompanying variation could be investigated with repeated sampling within short time spans. The assumption of no emigration or other losses is problematic, so each complete search should be carried out quickly (one to three nights) and repeated as often as expedient.

3. As conditions permit, snow tracking should be used to augment spotlighting. Data collected by snow tracking may not be directly comparable to spotlighting data. Because maximum comparability through standardization across sites and years is an important consideration, snow tracking may supplement spotlighting but cannot replace it. Ferret scats have been collected during snow tracking, providing additional opportunities for evaluations of food habits (Sheets and others, 1972; Campbell and others, 1987) and for molecular genetic assessments.

4. Telemetric monitoring will most likely provide con-

structive feedback for management decisions if used during the first release at a new site, at sites with high rates of ferret disappearance, during a dramatic population decline, or in studies designed to test hypotheses having wide-scale implications (see also Biggins, Godbey, Miller, and Hanebury, this volume). In the interest of avoiding additional burden to a dwindling population, it may be tempting to reduce monitoring intensity (and eliminate telemetry) at a time when information is most desperately needed. The information gained through detailed studies during a crisis may be critically important for future success at that site and for the recovery program in general. A "failure" may be recharacterized as a success if enough is learned to avoid repetition of the event at that same site or at other sites. As with snow tracking, use of radio telemetry does not eliminate the need for the spotlight surveys.

5. The addition of a spring spotlighting survey, conducted as described above for the fall and summer surveys, provides a useful assessment of overwinter survival and an estimate of the breeding population of ferrets. These surveys are often conducted in March or April (Matchett, 1997).

Other Issues—Duration of Monitoring Program, Altering the Intensity, Monitoring and Research

If the ferret population is not yet near estimated carrying capacity but its growth is as expected or above, the minimum monitoring strategy should be adequate. Because there will be a need to know when a population may require augmentation, and when a population is doing so well that it can be a source of animals for other populations, annual monitoring at these minimum levels should be conducted for each year that ferrets are released and at least 2 years following the final release. A ferret population may be surveyed in alternate years if it has a positive growth rate or remains stable because of birth of kits at the site for 2 years following the final release and if the site will not be serving as a source for translocations of ferrets. The most intensive monitoring should be planned for the first few years of releases at a site when there are many questions and no established record of success, with decreases in intensity during subsequent years. If population growth becomes slow or negative, intensive monitoring again is appropriate to identify the problem(s). Increased spotlighting and/or radio telemetry may be needed in some cases. Other types of monitoring (e.g., for diseases such as plague and distemper; prairie dog abundance and habitat quality) are also needed, and their results help define the relative need for ferret monitoring. The situation predictably will be dynamic, calling for flexibility in program management. If some working groups have insufficient resources to respond rapidly to changes, the leadership in the national program may need to recommend reallocation of resources (e.g., funds authorized under section 6 of the Endangered Species Act, different priorities for research support) to sites in response to shifting needs. Even the minimum monitoring standards proposed above may need modification if (1) the entire program becomes dramatically more or less successful than at present, (2) funding radically changes, (3) available habitat becomes fully occupied by ferrets, and (4) new technology makes more efficient techniques available. We strongly recommend close communication between working groups and national program managers during the process of formulating site-specific monitoring plans.

The suite of methods described for monitoring black-footed ferrets has been used for both research and management applications, but the distinction between the two purposes is poorly defined. Many ferret releases in the near future probably will have a blend of learning objectives (implying research with indirect benefits to long-term recovery) and population establishment objectives (implying management actions with direct, short-term benefits). A single monitoring program often contributes to both purposes. For example, snow tracking in 1982–86 at Meeteetse yielded winter population estimates for ferrets, helping to track the welfare of the population in the immediate sense, and gave information on movements of animals and other aspects of ecology (Richardson and others, 1987). Used during releases of ferrets, radio telemetry has allowed relocation of animals that dispersed into unsuitable habitat and has enabled documentation of heavy losses of ferrets to predation, information with important short-term management implications. In several cases, the primary purpose of radio telemetry was to test hypotheses of differential survival and behavior of groups of ferrets produced and released under varying conditions (Biggins and others, 1999). The minimum spotlighting standards recommended above emphasize the immediate need to assess population attributes. Addressing other objectives probably will require a more intensive strategy, expanded by adding other methods and/or increasing the amount of spotlighting (spatially or temporally).

References Cited

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., and Engeman, R.M., 1986, Aerial survey for black-footed ferret sign in snow, *in* Abstracts of contributed papers, 13th International Biometric Conference, Seattle, Wash.: Washington, D.C., International Biometric Society, p. 7.2.

Biggins, D.E., and Godbey, J.L., 2003, Challenges to reestablishment of free-ranging populations of black-footed ferrets: Comptes Rendus Biologies, v. 326, p. S104–S111.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Schroeder, M., Forrest, S., and Richardson, L., 1985, Movements and habitat relationships of radio-tagged black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 11.1–11.17.

Biggins, D.E., Schroeder, M.H., Forrest, S.C., and Richardson, L., 1986, Activity of radio-tagged black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 135–140.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Breck, S.W., and Biggins, D.E., 1997, Detecting and eliminating errors in radio-telemetry data sets—a comparison of screened and unscreened data [abs.], *in* Forum on wildlife telemetry—innovations, evaluations, and research needs: Jamestown, N. Dak., Northern Prairie Wildlife Research Center, U.S. Geological Survey, p. 15.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Campbell, T.M., III, Clark, T.W., Richardson, L., Forrest, S.C., and Houston, B.R., 1987, Food habits of Wyoming black-footed ferrets: American Midland Naturalist, v. 117, p. 208–210.

Clark, T.W., Campbell, T.M., III, Schroeder, M.H., and Richardson, L., 1984, Handbook of methods for locating black-footed ferrets: Cheyenne, Wyoming BLM Technical Bulletin No. 1, 55 p.

Fagerstone, K.A., Biggins, D.E., and Campbell, T.M., III, 1985, Marking and radiotagging of black-footed ferrets (*Mustela nigripes*), *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 10.1–10.10.

Fagerstone, K.A., and Johns, B.E., 1987, Transponders as permanent identification markers for domestic ferrets, black-footed ferrets, and other wildlife: Journal of Wildlife Management, v. 51, p. 294–297.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Fortenbery, D.K., 1972, Characteristics of the black-footed ferret: U.S. Fish and Wildlife Service, Resource Publication 109, 8 p.

Gaynor, J.S., Wimsatt, J., Mallinckrodt, C., and Biggins, D., 1997, A comparison of sevoflurane and isoflurane for short-term anesthesia in polecats: Journal of Zoo and Wildlife Medicine, v. 28, p. 274–279.

Heisey, D.M., and Fuller, T.K., 1985, Evaluation of survival and cause-specific mortality rates using telemetry data: Journal of Wildlife Management, v. 49, p. 668–674.

Henderson, F.R., Springer, P.F., and Adrian, R., 1969, The black-footed ferret in South Dakota: South Dakota Department of Game, Fish and Parks, Technical Bulletin 4, 37 p.

Hillman, C.N., 1968, Life history and ecology of the black-footed ferret in the wild: Brookings, South Dakota State University, M.S. thesis, 28 p.

Hines, J.E., Kendall, W.L., and Nichols, J.D., 2003, On the use of the robust design with transient capture-recapture models: Auk, v. 120, p. 1151–1158.

Hnilicka, P., and Luce, B., 1992, Post-release surveys of free-ranging black-footed ferrets in Shirley Basin during fall and winter of 1991–1992, *in* Oakleaf, B., Luce, B., Thorne, E.T., and Torbit, S., eds., 1991 annual completion report, black-footed ferret reintroduction, Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, p. 172–195.

Hnilicka, P., and Luce, B., 1993, Spotlighting and snowtracking surveys for free-ranging black-footed ferrets from 13 July 1992–11 January 1993 in Shirley Basin, Wyoming, *in* Oakleaf, B., Luce, B., Thorne, E.T., and Williams, B., eds., 1992 annual completion report, black-footed ferret reintroduction, Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, p. 158–187.

Hoogland, J.L., 1995, The black-tailed prairie dog—social life of a burrowing mammal: Chicago, University of Chicago Press, 557 p.

Hoss, K.A., Volz, T.A., Smith, L.R., Hackl, C.Z., Goodman, S.J., and Van Pelt, W.E., 2004, Results of the 2003 black-footed ferret release effort in Aubrey Valley, Arizona: Phoenix, Arizona Game and Fish Department, Nongame and Endangered Wildlife Program Technical Report, 20 p.

Hutchins, M., Wiese, R.J., and Bowdoin, J., 1996, Black-footed ferret recovery program analysis and action plan: Bethesda, Md., American Zoo and Aquarium Association, 137 p.

Kendall, W.L., Pollock, K.H., and Brownie, C., 1995, A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design: Biometrics, v. 51, p. 293–308.

Kreeger, T.J., Vargas, A., Plumb, G.E., and Thorne, E.T., 1998, Ketamine-medetomidine or isoflurane immobilization of black-footed ferrets: Journal of Wildlife Management, v. 62, p. 654–662.

Lebreton, J.D., Burnham, K.P., Clobert, J., and Anderson, D.R., 1992, Modeling survival and testing biological hypotheses using marked animals—a unified approach with case studies: Ecological Monographs, v. 62, p. 67–118.

Lehmer, E.M., Van Horne, B., Kulbartz, B., and Florant, G.L., 2001, Facultative torpor in free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*): Journal of Mammalogy, v. 82, p. 552–557.

Luce, B., Hunter, L., and Oakleaf, B., 1994, Spotlighting and snowtracking surveys for free-ranging black-footed ferrets from 25 July–30 November 1993 in Shirley Basin, Wyoming, *in* Luce, B., Oakleaf, B., Thorne, E.T., and Williams, E.S., eds., 1993 annual completion report, black-footed ferret reintroduction, Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, p. 63–96.

Marinari, P.E., 1992, Detectability of black-footed ferrets (*Mustela nigripes*) using spotlighting: Laramie, University of Wyoming, M.S. thesis, 123 p.

Matchett, R., 1997, Annual report of black-footed ferret recovery activities, UL Bend and Charles M. Russell National Wildlife Refuges, southern Phillips County, Montana: Lewistown, Mont., U.S. Fish and Wildlife Service, 71 p.

Miller, B.J., and Biggins, D.E., 1988, Winter monitoring of black-footed ferrets (*Mustela nigripes*): Fort Collins, Colo., U.S. Fish and Wildlife Service, 17 p.

Otis, D.L., Burnham, K.P., White, G.C., and Anderson, D.R., 1978, Statistical inference from capture data on closed animal populations: Wildlife Monographs 62, 135 p.

Plumb, G.E., and Marinari, P.E., 1996, Black-footed ferret monitoring in Badlands National Park, September 1994–September 1995, *in* McDonald, P.M., Marinari, P.E., and Plumb, G.E., eds., Black-footed ferret reintroduction: year one completion report, Conata Basin, Badlands, South Dakota: Wall, S. Dak., U.S. Forest Service, p. 94–115.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., and Curtis, P.D., 1989, Survival analysis in telemetry studies—the staggered entry design: Journal of Wildlife Management, v. 53, p. 7–15.

Reindl, S.A., 2004, Efficacy of scent dogs in detecting black-footed ferrets (*Mustela nigripes*) at a reintroduction site in South Dakota: Brookings, South Dakota State University, M.S. thesis, 60 p.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming: American Midland Naturalist, v. 117, p. 225–239.

Rivest, L.P., and Daigle, G., 2004, Loglinear models for the robust design in mark-recapture experiments: Biometrics, v. 60, p. 100–107.

Sheets, R.G., 1972, A trap for capturing black-footed ferrets: American Midland Naturalist, v. 88, p. 461–462.

Sheets, R.G., Linder, R.L., and Dahlgren, R.B., 1972, Food habits of two litters of black-footed ferrets in South Dakota: American Midland Naturalist, v. 87, p. 249–251.

Staley, G., and Luce, B., 1995, Spotlighting and snowtracking surveys for free-ranging black-footed ferrets from 25 July 1994–15 February 1995 in Shirley Basin, Wyoming, *in* Luce, B., Oakleaf, B., Thorne, E.T., and Williams, E.S., eds., 1994 annual completion report, black-footed ferret reintroduction, Shirley Basin, Wyoming: Cheyenne, Wyoming Game and Fish Department, p. 34–69.

Stoneberg, R., 1996, Implanted microchips used to individually identify black-footed ferrets in Montana: Prairie Naturalist, v. 28, p. 163–168.

Thorne, E.T., Schroeder, M.H., Forrest, S.C., Campbell, T.M., III, Richardson, L., Biggins, D., Hanebury, L.R., Belitsky, D., and Williams, E.S., 1985, Capture, immobilization and care of black-footed ferrets for research, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 9.1–9.8.

U.S. Fish and Wildlife Service, 1988, Black-footed ferret recovery plan: Denver, Colo., U.S. Fish and Wildlife Service, 154 p.

White, G.C., Anderson, D.R., Burnham, K.P., and Otis, D.L., 1982, Capture-recapture and removal methods for sampling closed populations: Los Alamos, N. Mex., Los Alamos National Laboratory, 235 p.

White, G.C., and Burnham, K.P., 1999, Program MARK—survival estimation from populations of marked animals: Bird Study, v. 46 (suppl.), p. 120–138.

White, G.C., and Garrott, R.A., 1990, Analysis of wildlife radio-tracking data: San Diego, Calif., Academic Press, 383 p.

Winstead, R.A., Hoss, K.A., Volz, T.A., Hooge, J., Smith, L., and Van Pelt, W.E., 2003, Results of the 2002 black-footed ferret release effort in Aubrey Valley, Arizona: Phoenix, Arizona Game and Fish Department, Nongame and Endangered Wildlife Program Technical Report, 26 p.

Appendix. Forms, Checklists, and Other Information that May Be Useful When Spotlighting, Capturing, and Handling Black-footed Ferrets

Spotlight Schedule/Assignments

Night of: ____________________

Hours: ____________________

Name	PDTs/route	Vehicle	No. of readers	Radio	Missing BFF/other

Black-footed Ferret (BFF) Survey Form

Mark sequential observation numbers on reverse-side map. Flag each location with BFF ID, date, and time for later GPS mapping.

Observer: ______________________ Night of: ______________________
(e.g., 3/19–20/98)

Transportation type: ______________________

Prairie dog colony: (Sketch area searched on map on reverse side.)

Cloud cover: ______________________ Moon phase: ______________________

Snow cover %: ____________ Temp.: ________ Wind speed/direction: ____________

Comments: ____

Start and end time	Map and observation number	Time seen	BFF ID	Transponder number	Location	Time trap set/checked	Predators observed

Total search minutes: ____________

Black-footed Ferret Markings

ID	Sex	Date	Head transponder	Pelvis transponder	Dye	Location	CDV

Black-footed Ferret Handling Checklist

1. __________Verify lack of transponder, other markings, and need to handle

2. __________Date ________Time ________ Sex ________ Age ________ ID

3. __________Dam ________ Stud ________ Location and plot on map

4. __________Trapper ________ Team

5. __________Anesthetize at 3.0–4.0 ISO ________ Time

6. __________DIAL ISOFLURANE TO 1.75, transfer to face mask ________ Time

7. __________PATIENT NO.

Time	ISO	Oxygen	Pulse rate	% oxygen saturation	Respiration rate	Temperature

8. __________ Implant transponder chips HEAD ______________ PELVIS ______________
9. __________ Test transponder chips
10. __________ Collect hair and label envelope
11. __________ Collect blood and label VACUTAINER (cc) __________ NOBUTO (y/n) _______
12. __________ Give 1 cc, SC canine distemper vaccine. If recapture, booster given at 2 weeks
13. __________ Give penicillin injection (<1,000 g = 0.3 mL SC| >1,000 g = 0.4 mL SC)
14. __________ Apply dye mark: ADULT MALE = ---- WILD MALE = X OTHER
    ADULT FEMALE = | WILD FEMALE = 0
15. __________ Health inspection notes, read old tattoo, teeth, anomalies, etc.

16. __________ ISOFLURANE AND OXYGEN OFF
17. __________ Weigh
18. __________ Monitor recovery
19. __________ Disinfect/clean all equipment and surfaces, prepare for next animal

Dosages of Injectable Anesthetics for Black-footed Ferrets

KETAMINE/DIAZEPAM DOSAGES
premixed 10 mL KET (1,000 mg) with
2 mL DIAZEPAM (10 mg)

MEDETOMIDINE/KETAMINE
3.0 mg/kg KETAMINE + 0.075 mg/kg MEDETOMIDINE
Antagonize with 0.45 mg/kg; ATIPAMEZOLE after ≥30 min

Weight (g)	Light (20 mg/kg; cc)	Medium (25 mg/kg; cc)	T/T dose (30 mg/kg; cc)	Heavy (35 mg/kg; cc)	KET (cc)	MED (cc)	TOT (cc)	ATI (cc)
100	0.020	0.025	0.030	0.035	0.075	0.038	0.11	0.045
200	0.040	0.050	0.060	0.070	0.150	0.075	0.23	0.090
300	0.060	0.075	0.090	0.105	0.225	0.113	0.34	0.135
400	0.080	0.100	0.120	0.140	0.300	0.150	0.45	0.180
500	0.100	0.125	0.150	0.175	0.375	0.188	0.56	0.225
600	0.120	0.150	0.180	0.210	0.450	0.225	0.68	0.270
700	0.140	0.175	0.210	0.245	0.525	0.262	0.79	0.315
800	0.160	0.200	0.240	0.280	0.600	0.300	0.90	0.360
900	0.180	0.225	0.270	0.315	0.675	0.338	1.01	0.405
1,000	0.200	0.250	0.300	0.350	0.750	0.375	1.13	0.450
1,100	0.220	0.275	0.330	0.385	0.825	0.412	1.24	0.495
1,200	0.240	0.300	0.360	0.420	0.900	0.450	1.35	0.540
1,300	0.260	0.325	0.390	0.455	0.975	0.488	1.46	0.585
1,400	0.280	0.350	0.420	0.490	1.050	0.525	1.58	0.630
1,500	0.300	0.375	0.450	0.525	1.125	0.562	1.69	0.675

$$\text{DOSAGE} = \frac{\text{BODY WEIGHT * DOSE}}{\text{CONCENTRATION}}$$

MED/KET CONCENTRATIONS: KET = 4.0 mg/mL
MED = 0.2 mg/mL
ATI = 1.0 mg/mL

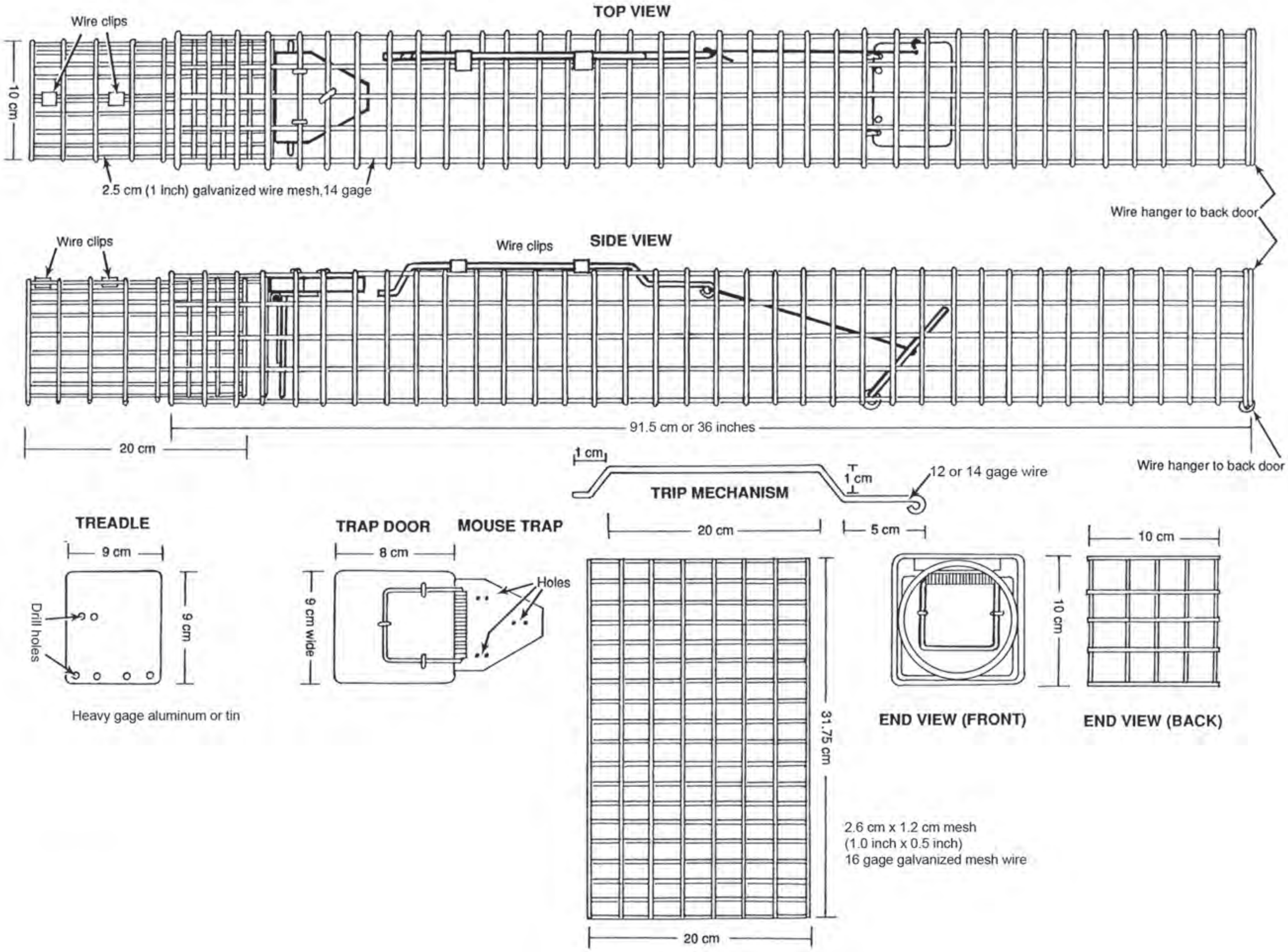

Figure A1. Design of a trap for black-footed ferrets (*Mustela nigripes*). This trap is a modification of the model described by Sheets (1972).

Radio Telemetry for Black-footed Ferret Research and Monitoring

By Dean E. Biggins,[1] Jerry L. Godbey,[1] Brian J. Miller,[2] and Louis R. Hanebury[3]

Abstract

By 1973, radio telemetry was regarded as an important potential tool for studying the elusive, nocturnal, and semifossorial black-footed ferret (*Mustela nigripes*), but fears of using invasive techniques on this highly endangered mammal caused delays. We began radio collaring ferrets in 1981. Use of radio telemetry on ferrets proved to be both challenging and rewarding. We document two decades of development and use that led to the present radio-tagging techniques and methods for radio tracking. The 7-g radio collar commonly used after 1992 was smaller and lighter, relative to mass and size of subjects, than collars used in studies of other *Mustela*. Other important developments were a Teflon® coating to shed mud, a highly flexible stainless steel cable for whip antennas, and a nondurable wool collar. Although collar-caused neck abrasions have continued to occur sporadically, a retrospective assessment of minimum survival rates for 724 reintroduced ferrets (392 radio tagged), using data from spotlight surveys, failed to detect negative effects of radio-collars. In a South Dakota study, ferrets that were found to have hair loss or neck abrasions when collars were removed did not exhibit movements significantly different from those of radio-tagged ferrets with no evidence of neck problems. Prototype transmitters designed for surgical implantation had insufficient power output for effective use on ferrets. Early attempts at tracking radio-tagged ferrets by following the signal on foot quickly gave way to following movements by triangulation, which does not disturb the subjects. The most effective tracking stations were camper trailers fitted with rotatable, 11-element, dual-beam Yagi antennas on 6-m masts. We used radio telemetry to produce 83,275 lines of data (44,191 indications of status and 39,084 positional fixes via triangulation) for 340 radio-collared ferrets during the reintroduction program. Tracking by hand and from aircraft augmented triangulation, allowing us to locate animals that dispersed long distances and enabling us to determine causes of mortality. Justifying further use of radio telemetry on black-footed ferrets requires careful consideration of costs and benefits.

Key words: black-footed ferret, collar, *Mustela eversmannii*, *Mustela nigripes*, radio telemetry, radio tracking, Siberian polecat, survival, triangulation

Introduction

Radio telemetry has been used as a tool to study vertebrates for more than 50 years (Kimmich, 1979) and *Mustela* since the mid-1970s (Erlinge, 1979). The technique is especially useful for re-locating individual animals that are highly mobile, secretive, and difficult to observe. Black-footed ferrets (*M. nigripes*) are among the most nocturnal of carnivores, and they are semifossorial, attributes that reduce our ability to monitor them with other techniques. Ferrets may be located with spotlights, a technique that is often employed for conducting annual surveys of their abundance (Campbell and others, 1985; Biggins and others, 1998a). Spotlighting, however, affects the behaviors of ferrets (Campbell and others, 1985), making it less attractive for the intensive monitoring that may be required for behavioral studies. Techniques must be matched to objectives, and the relative advantages and disadvantages of radio telemetry, spotlighting, and snow tracking for studying black-footed ferrets have been summarized elsewhere (Biggins, Godbey, Matchett, and others, this volume). This article addresses the challenges of applying radio telemetry to studies of black-footed ferrets, in part to help a potential investigator decide whether it is the appropriate tool for the goals of the project being considered.

Because of difficulties encountered by earlier researchers in studying this secretive species and because technologies were rapidly advancing, radio telemetry was recognized as a "vital" tool for future ferret investigations (commentary by E. Brigham in Linder and Hillman, 1973, p. 162). Erickson (1973, p. 156) emphasized a need to use radio telemetry on ferrets, lamenting that "the black-footed ferret is one of the least well known of all of the endangered mammals of the United States, despite 10 years of intensive research." The anticipated importance of this tool was reflected in a primary objective of the first captive breeding program for

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black-footed ferrets (commencing in 1971), which was “not to produce animals for release in the wild, but to learn more about . . . safe marking methods” and “means of following their travels and home range” (commentary by R. Erickson in Linder and Hillman, 1973, p. 26). These experiences of the 1970s motivated development of prototype transmitters for black-footed ferrets, but, by the latter years of that decade, no free-ranging ferrets could be found. Our use of radio telemetry on black-footed ferrets began in 1981 with the discovery of the last known extant population west of Meeteetse, Wyo. Our intent is to review the use of radio telemetry for black-footed ferret research during the subsequent two decades. There is a particular need to document the problems and our attempts to find solutions. Detailed discussions of hardware and methods that did not work seem as important as discussion of the triumphs, if only to provide a better starting point for those who might wish to engage in improving the techniques. We review the challenges of radio tagging these animals, methods used to gather data once they have been tagged, and methods for analyzing those data.

Radio Tagging Black-footed Ferrets

In a prophetic prediction of upcoming problems, Erickson (1973, p. 157) stated “There is no known way to safely develop and test methods of installing radio-transmitter harnesses on live ferrets in the wild.” Although the first transmitter packages intended for use on black-footed ferrets (fig. 1) were indeed tested on surrogate domestic ferrets (*M. putorius furo*; fig. 2) (C. Hillman and S. Martin, oral commun., 1980), problems developed when the collars were first used on black-footed ferrets at Meeteetse in 1981–82. Neck abrasions sometimes occurred with these 15-g collars, and they had low power output (table 1, version A-1), in part caused by the inefficient brass loop antenna that also served as a collar (fig. 1). The low power resulted in frequent loss of contact with subjects (Fagerstone and Biggins, 1986). Although a more powerful collar prototype was produced in 1982 (table 1, version B-1), it seemed too bulky for use on ferrets. That transmitter was attached to a harness, but tests on surrogate prairie dogs (*Cynomys* spp.) (fig. 3) were unsuccessful. The original packages were again used in 1982, but the brass loop collars were difficult to fit and collar loss was high (Fagerstone and Biggins, 1986). These first radio collars for ferrets transmitted on 164 MHz.

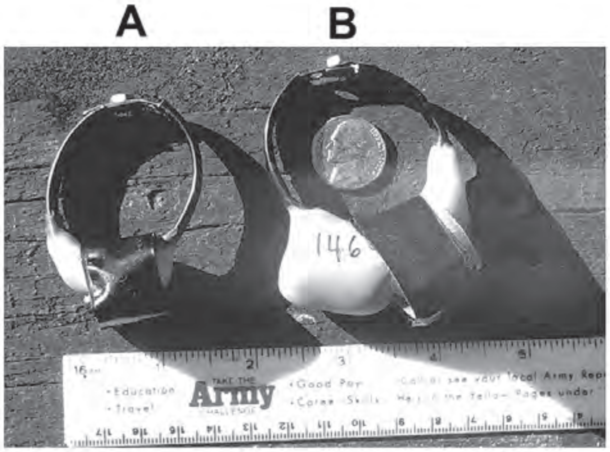

Figure 1. The first radio collars tested for use on black-footed ferrets (*Mustela nigripes*), ca. 1979 (version A-1 of table 1). A model similar to “A” was used on ferrets. Photograph by D. Biggins.

Figure 2. Early transmitter packages with tuned loop antennas (version A-1 of table 1) were tested on domestic ferrets (*Mustela putorius furo*). Photograph by U.S. Fish and Wildlife Service.

We also conducted comparative experiments with reception of signals emanating from underground transmitters on 30 MHz and 164 MHz, reasoning that the longer wavelengths would better penetrate soil. The lower frequencies performed no better than the higher frequencies during underground trials, but problems with transmitting and receiving antennas were exacerbated with the lower frequencies (lower frequencies need larger antennas for efficient transmission and reception). All subsequent transmitters were on 164–165 MHz at frequencies licensed to the U.S. Department of the Interior.

Early in 1983 we submitted specifications for a new transmitter collar to manufacturers of wildlife telemetry equipment, requesting their assistance in producing an improved transmitter package. Prototypes from three of the five companies that responded exceeded dimensional or weight limits. Two units (table 1, version D-1, fig. 4; table 1, version C-1, fig. 5) seemed satisfactory and were used on 10 black-footed ferrets in August 1983 (Fagerstone and Biggins, 1986). Reception range was several times greater with model D-1 than with model A-1 used in 1981–82. During 1983, however, breakage of the whip antenna was common, and sometimes accumulations of clay resulted in large increases in mass and dimensions of the transmitter package (fig. 6). The accumulations of clay likely were partially responsible for some neck injuries. Various treatments and coatings, including polished acrylic (fig. 7A), wool (fig. 7B), and Teflon® (DuPont, Wilmington, Del.) heat-shrink tubing (fig. 8), were used in laboratory trials and on prairie dogs and ferrets in the field during 1983 and 1984 to alleviate the mud accumulation problem (Fagerstone and Biggins, 1986). The Teflon tubing solved the problem of mud accumulation; however, its slippery surface seemed to

Table 1. Transmitter packages tested during development of radio-telemetry applications for black-footed ferrets (*Mustela nigripes*).

Version	Year	Type	Weight (g)	Antenna	Effective power[1]	Pulse		Battery life (days)
						Width[2]	Rate[3]	
A-1	1981	collar	15	14.0-cm loop	-35		104	100
B-1	1982	harness		44.5-cm whip	-9	14	34	
C-1	1983	collar	10	8.9-cm whip	-35	104	30	39
D-1	1983	collar	13	15.2-cm whip	-12	25	66	
E-1	1983	collar		16.5-cm whip	-40		19	
D-2	1989	collar	10	15.2-cm whip	-18	11–40	25–67	59+
A-2	1991	collar	9	20.3-cm whip			variable	variable
D-3	1992	collar	7	20.3-cm whip	-20	25	47	50
D-4	1985	implant	18	internal coil	-41		47	
D-5	1985	implant	4	whip	-37		80	
E-2	1985	implant	26	internal coil	-39		60	

[1] Decibels relative to 1 milliwatt (dBm).

[2] Milliseconds duration.

[3] Pulses per minute.

Figure 3. Capsules with high power output (Telonics, Inc., Mesa, Ariz.) (version B-1 of table 1) were attached to harnesses and tested on surrogate prairie dogs (*Cynomys* spp.) in 1982. Photograph by D. Biggins.

Figure 5. A package coated with soft plastic used on black-footed ferrets (*Mustela nigripes*) in 1983 (version C-1 of table 1). Photograph by D. Biggins.

Figure 4. A 13-g transmitter package (version D-1 of table 1) used on black-footed ferrets (*Mustela nigripes*) during 1983–84. Photograph by D. Biggins.

exacerbate collar loss, and there were several instances of neck abrasions.

Continued problems with collar loss in 1984 motivated additional investigation and development of transmitter attachment methods for ferrets. Disease outbreaks in Meeteetse prairie dogs and ferrets (Forrest and others, 1988; Ubico and others, 1988) ended all hope for continued research on that free-ranging population of ferrets; however, the ensuing captive breeding program and its ultimate goal of reintroductions underscored the importance of improving radio telemetry for ferrets. In trials conducted in the spring of 1985, two of three free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*) developed neck sores when fitted with old-style ferret collars made of vinyl-impregnated cloth but did not seem adversely affected by neckbands of wool (*n* = 4) or leather (*n* = 4). Prairie dogs gained 40 percent in mass during a 3-month period. Wool collars sewed with cotton thread often wore sufficiently to be lost by prairie dogs in 3 to 6 months. Thus, a black-footed ferret with a wool

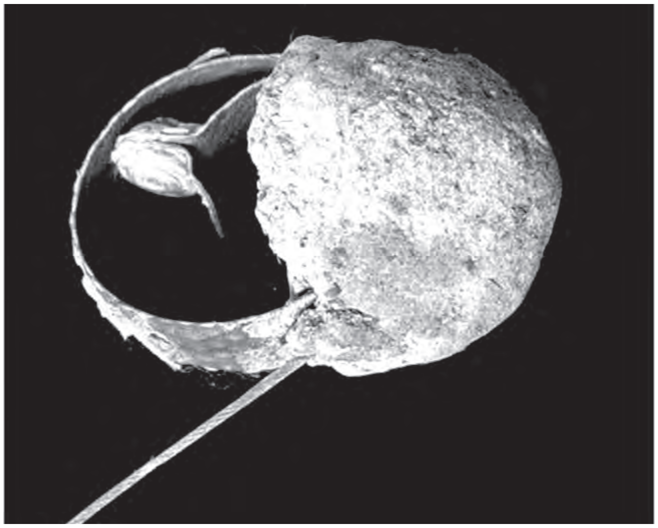

Figure 6. A collar from 1983 that accumulated a large buildup of clay while carried by a black-footed ferret (*Mustela nigripes*). Photograph by D. Biggins.

neckband would not be collared permanently if its radio failed prematurely and the animal could not be relocated for collar removal.

One of the goals of research initiated in 1988 on Siberian polecats (*Mustela eversmannii*) and other surrogate species was to advance our proficiency in radio tagging and radio tracking *Mustela* before reintroductions of black-footed ferrets. Studies of captive Siberian polecats and of reproductively sterilized polecats released into prairie dog colonies in Colorado and Wyoming provided opportunities to develop and test equipment. Radio collars made of natural materials were first tested on 13 captive polecats at the National Zoo's Conservation & Research Center, Front Royal, Va., during September 1989. Neckbands were made of leather or wool instead of the vinyl-coated fabric used previously. Collar retention was the primary reason for preliminary testing of radio collars on captive ferrets. Wool and leather collars are somewhat elastic, and the >10 percent stretch of these materials might allow animals to slip out of the collars. Overlapping ends of wool and leather collars were glued with contact cement. The transmitter package for polecats weighed about 10 g, had a 15.2-cm whip antenna (table 1, version D-2), and was attached to a 1-cm-wide wool collar with vinyl tape (not Teflon). The 2-stage, 3-V transmitter had a mercury switch that triggered change in pulse rate, resulting in pulse intervals of about 0.9–2.4 seconds, with pulse interval inversely proportional to activity of the animal (as sensed by motion of the transmitter), and a pulse width inversely proportional to pulse interval to maintain consistent and predictable current drain. Battery longevity was about 59 days.

Both wool and leather collars were removed by some captive animals, but in most cases the shed collars were in poor condition. Captive polecats were housed in family groups and tended to chew and pull on each other's collars causing rapid wear that we did not expect to occur under field

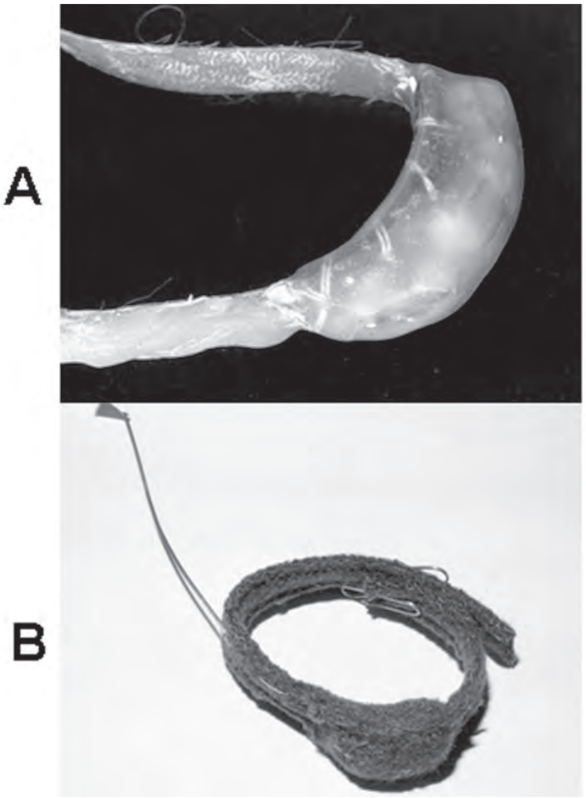

Figure 7. The acrylic potting material was polished (A) or encased in wool (B) in attempts to alleviate mud accumulation. Photograph by D. Biggins.

Figure 8. A 13-g transmitter package (version D-1 of table 1) from Wildlife Materials, Inc. (Murphysboro, Ill.), with Teflon tubing covering most of the acrylic potting material (used on black-footed ferrets [*Mustela nigripes*] during 1984). Photograph by D. Biggins.

conditions. Wool collars were no more likely to be pulled off than were leather collars, but wool collars wore more quickly. Because the “breakaway” feature of wool was desirable, the wool collar was selected for testing on the released animals to evaluate retention and irritation. Under field conditions, only 1 of the 13 polecats removed its collar, but that animal did so twice. Whip antennas broke on collars worn by two polecats. One antenna became completely severed after 10 days on the animal, and a radio recovered from a dead polecat had several broken strands in its antenna wire. Our simple solution was to use slightly heavier wire and an extra layer of heat-shrink coating extending 1 cm above the point where the antenna protruded from the radio capsule. No sign of worn hair or neck abrasion was noted on recovered polecats; however, there were only a few days of wet weather during our polecat release study, and the soil was sandier than soil at the Meeteetse black-footed ferret study area. Therefore, the potential for mud accumulation on radio collars was not fully assessed. During a short wet period, a small amount of mud was found on the collar of one recaptured polecat, but the mud fell away easily. Poor survival of polecats hampered the evaluation of radio-collar performance in that study (Biggins, 2000a).

Additional polecats released in 1990 ($n = 44$) accumulated about 600 animal days wearing the type of radio collars described above (but with the modified antennas), combining the time that animals carried radio collars during arena conditioning with monitoring time after release. The wool collars continued to function well overall. One collar deteriorated rapidly and was lost from a polecat after only 2 weeks, perhaps because that animal (no. 34, wild caught in China) was exceptionally active. Several other animals lost collars, likely in part because of rapid weight loss after release, particularly with obese animals (Biggins, 2000a). One instance of neck abrasion was noted, and again it was with animal no. 34. That animal was recollared after losing her first transmitter collar; perhaps the tendency was to fit the second collar too tightly because of the prior loss.

The polecat from China (no. 34), radio tracked until the study ended, lost 50 percent of her body mass and her radio collar during the first several weeks postrelease. Perhaps that scenario helps explain the high rate of lost radio contact with wild-caught polecats (3/5 versus 5/39 for captive-bred polecats). Other factors also can cause loss of radio contact. Two recovered radio collars were damaged, presumably by the teeth of coyotes (*Canis latrans*). The signal from one of those collars was barely audible above ground, even at short range (<100 m), suggesting the possibility of complete radio failure from bites of coyotes or badgers (*Taxidea taxus*). Radio signals also can be lost when animals are in burrows >2 m below ground. Because loss of radio contact could have been a result of predation, dispersal, or premature transmitter failures, functional longevity for collars could not be estimated.

Similar versions of these transmitters with wool collars also were used to study free-ranging Siberian polecats (fig. 9) (Zhou and others, 1994) and alpine weasels (*Mustela altaica*) in China (fig. 10). Collars of wool functioned well generally, but premature collar loss and occasional neck abrasions continued to be problems. Collar loss was especially common in the alpine weasel study (Wei and others, 1996). The polecat transmitter packages with variable pulse rates used in China and the United States produced easily interpreted activity data.

Figure 9. Additional collar tests (version D-2 of table 1) were conducted on a subspecies of free-ranging Siberian polecat (*Mustela eversmannii dauricus*) in Inner Mongolia, China. Photograph by D. Biggins.

Figure 10. We used smaller transmitters with wool collars to study alpine weasels (*Mustela altaica*) in Qinghai, China. Photograph by D. Biggins.

Because of the effective combination of wool collars and activity-type transmitters used on polecats, this 10-g unit by Wildlife Materials, Inc., (WMI, Murphysboro, Ill.) and a similar variable-pulse rate model by AVM Instrument Company, Ltd., (Colfax, Calif.) (table 1, version A-2) were adopted for monitoring 37 of 49 black-footed ferrets released during the first reintroductions in 1991 at Shirley Basin, Wyo. (U.S. Fish and Wildlife Service, 1992). Collars were worn by ferrets for 2–4 weeks before they were released, allowing prerelease observation of animals but also expending 40–68 percent of the expected battery life and producing noticeable wear to the wool collars.

Fluctuations in mass of animals appeared to create problems. Ferrets from the Henry Doorly Zoo (Omaha, Nebr.) were 26 percent heavier when collared than were their wild counterparts at Meeteetse ($P < 0.001$) and were 37 percent heavier at 5 days postcollaring. Seven of the zoo ferrets developed neck sores while being held in cages, perhaps because of the increasingly snug fit of the collars as the ferrets gained mass. Ferrets raised at the Wyoming Game and Fish Department facility were not heavier than Meeteetse ferrets prerelease. We accumulated 460 animal days of postrelease telemetric monitoring on the 37 ferrets. Loss of mass postrelease (Biggins, 2000a) likely loosened the fit of collars and may have exacerbated premature collar loss that occurred in nine known instances involving six individual ferrets (ferrets were sometimes recollared). One free-ranging ferret had a neck laceration when recaptured, but other injuries confused determination of the cause(s). There were two known cases of mud adhering to the vinyl tape used to attach the transmitter package to the collar.

Continued problems with collars in 1991 resulted in a more conservative approach to collar configurations used for ferret studies in subsequent years. Beginning in 1992, ferrets were collared with smaller transmitter packages, and Teflon heat-shrink tubing became the standard method for attaching the transmitter to the double- or triple-layered wool collar (fig. 11). The WMI transmitter had a 20.3-cm flexible steel whip antenna (table 1, version D-3). We located an improved type of stainless steel wire for whip antennas (designed for operating prosthetic limbs) that further reduced the problem of breakage resulting from metal fatigue. The 1.5-V battery gave an estimated 45–150 days of transmitting, depending on power output desired. The completed package weighed 6.0–7.2 g (usually <1 percent of the subject's mass). We believe that miniaturization of the transmitter-collar assembly reduced problems of collar loss and neck abrasion in black-footed ferrets. See appendix for instructions on final assembly of these collars and the procedure for fitting them to ferrets.

Figure 11. Fitting a lightweight (6–7 g) transmitter collar (version D-3 of table 1) to a black-footed ferret (*Mustela nigripes*). This style of collar has been used since 1991. Photograph by R. Reading.

Serious neck injuries may be caused by improper fit of radio collars; abrasions on radio-collared black-footed ferrets in 1991 fueled controversy over effects of collars on survival of ferrets. Oakleaf and others (1993), using data generated from spotlight searches after the second ferret release in 1992, stated that "survival indices are significantly ($P = 0.002$–0.055) greater for black-footed ferrets released without telemetry compared to ferrets released with telemetry collars." These authors presented four criteria that should be met to enhance comparability of collared and noncollared groups in future studies. Data for their analyses were generated under conditions that violated two of their criteria, similarity in habitat quality and equal accessibility for spotlight searches in areas where radio-collared and noncollared ferrets are released. Radio-collared ferrets were released on lower quality habitat, as measured by densities of prairie dog burrows, than were noncollared ferrets, and the areas with collared ferrets were less easily searched via spotlighting. Prior recognition of the possibility of confounding can be inferred from the hypothesis generated before the 1992 release of ferrets, which stated that "survival of ferrets released in best habitat, without telemetry and with good logistics for spotlight surveys is higher than survival in habitat that is possibly less than the best, with telemetry, and possibly poorer conditions for spotlighting" (B. Oakleaf, quoted in Miller and others, 1996, p. 129). Regarding habitat quality, mounting evidence demonstrates a negative correlation between ferret dispersal and density of prairie dog burrows (Biggins and others, 1999; Biggins, 2000b), and ferrets prefer areas with high burrow density (Biggins, Godbey, Matchett, and Livieri, this volume).

Confounding of collar effect and other variables was problematic in the 1992 sample involving 89 ferrets but became less troublesome as sample size increased because the potentially confounding variables were not consistently associated with the same primary treatment groups. Thus, it may be revealing to examine a much larger data set of reencounters, resulting from spotlight surveys about 1 month postrelease, for 724 ferrets released in four States during 12 years (table 2). For all States except Wyoming, cage-reared ferrets were excluded from the analysis because ferrets that lack preconditioning in outdoor pens have relatively poor survival rates (Biggins and others, 1998a). We could not categorize rearing status for some of the ferrets released in Wyoming; thus, we pooled rearing categories in Wyoming (similar to the analysis of Oakleaf and others, 1993). A multivariate general model (with site-year and mark category) and competing nested submodels were evaluated with program SURVIV (White, 1983). Comparisons of Akaike's Information Criteria (AIC) associated with these models (table 3) favored either the submodel that pooled collared and noncollared ferrets (AIC = 52.86) or the general model (AIC = 51.14). Not surprisingly, reencounter rates (the product of probabilities of survival and capture) for sites-years were likely different. Although

Table 2. Numbers of black-footed ferret (*Mustela nigripes*) kits released with and without radio collars. Assessment included only preconditioned kits (except in Wyoming).

	Montana		South Dakota		Utah		Wyoming		
Year	**No radio**	**Radio**	**No radio**	**Radio**	**No radio**	**Radio**	**No radio**	**Radio**	**Total**
1991							12	37	49
1992							52	37	89
1993							48		48
1994		17	7	6			37		67
1995		35		37					72
1996	28			39					67
1997			2	57					59
1998			41	42					83
1999				30	35	18			83
2000					27	29			56
2001					35	8			43
2002					8				8
Total	28	52	50	211	105	55	149	74	724

Table 3. Modeling minimum short-term (1 month) survival rates of 392 radio-collared and 332 noncollared black-footed ferrets (*Mustela nigripes*) released in Montana, South Dakota, Utah, and Wyoming.

Model	Log-likelihood	np[a]	AIC[b]
General	-17.534357	8	51.06871
All same	-92.542614	1	187.08523
Collaring same	-22.228649	4	52.45729
Sites-years same	-85.786658	2	175.57332

[a] np = number of parameters.

[b] AIC = Akaike's Information Criterion.

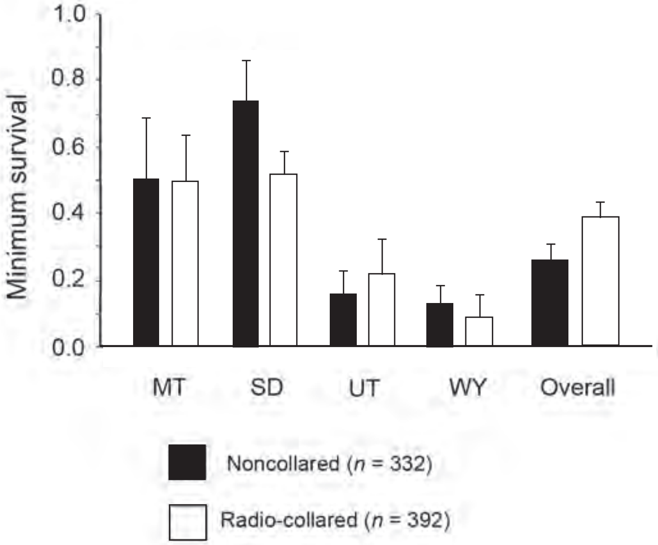

Figure 12. Minimum survival rates of preconditioned black-footed ferret (*Mustela nigripes*) kits at about 1 month postrelease.

evidence was somewhat equivocal regarding collars, the most parsimonious model of the two with low AIC values suggested no effect of collars (fig. 12). Regardless of improvements in sample size and reduced confounding potential, this remains a post hoc analysis of data from experiments designed to test other hypotheses. Interactions are probable (fig. 12) and the unbalanced design (table 2) allows numerous possible explanations to account for the disparate results for different sites and years. Nevertheless, these data do not support the contention that radio collars negatively affect reencounter rates of released black-footed ferrets. Perhaps cases of management intervention enabled by radio telemetry help compensate for potentially negative influences of collars. On a few occasions, ferrets that dispersed from suitable habitat were captured and translocated; other interventions (also rare) included capture, rehabilitation, and rerelease of ferrets that were injured or in poor condition.

In a study of translocated ferrets conducted in South Dakota in 1999 (Biggins and others, 2000a), neck abrasions that ranged from minor hair loss to a case of severe ulceration were noted on 10 radio-tagged black-footed ferrets (of 36 released) when animals were reobserved during the study or recaptured for collar removal at the end of the study. A categorical variable (abrasion, no abrasion) for neck condition was evaluated during statistical modeling to assess movements and dispersal of the primary treatment groups (released captive-reared versus wild-born ferrets). There was no evidence that neck abrasions affected any of the attributes of movements examined ($P > 0.19$ for all models), even though the experimental design and statistical analyses were sufficiently powerful to detect significant effects of several other variables.

In summary, collar-caused mortality of ferrets has not been documented, and there is no evidence of negative effects of radio telemetry on ferret populations or average behaviors within groups of ferrets. Nevertheless, collaring can at times negatively impact individual ferrets. Moreover, it seems best to assume, even without the latter evidence, that an unnatural protuberance of any sort will influence a free-ranging animal's behavior to some degree, even if that influence is not detectable statistically. Such influences may be acceptable, particularly if it can be reasonably assumed that they equally affect all treatment groups of an experiment. Decisions on whether or not to use this monitoring tool may rest with cost/benefit analyses. If information potentially gained could enhance success of future conservation of the ferret, risk to individuals may be warranted. The arguments, however, appear similar to those discussed with reference to releasing adult ferrets (Biggins, Godbey, Livieri, and others, this volume), wherein "some conservationists and ethicists may justify extreme means to achieve the goal of preservation and recovery" of a species, while "others may set inviolate moral standards regarding the welfare of individuals."

Compared to other recent studies of *Mustela* that have involved radio telemetry, our present collars have rather conservative dimensions and mass. Considering *Mustela* of sizes similar to black-footed ferrets, 27-g and 25-g collars were fitted to feral domestic ferrets in New Zealand (Moller and Alterio, 1999; Byrom, 2002), collars of 25–35 g were placed on European polecats (*M. putorius*) in Italy (Marcelli and others, 2003), and endangered European mink (*M. lutreola*) were tagged with collars of about 13 g in Spain (Zabala and others, 2003). Collars weighing 10 g (likely 4–6 percent of body mass) were placed on stoats (*M. erminea*) in New Zealand (Moller and Alterio, 1999). Although Jedrzejewski and others (2000) tagged least weasels (*M. nivalis*) in Poland with collars of only 3.5–4.5 g, that mass was about 4 percent of the body mass of their subjects. Realizing the sensitivity of these animals to handling and collaring, the latter investigators placed the weasels into an enclosure for several days of observation before final release at the location of capture. We are aware of problems of collar loss and neck abrasion caused by radio collars in other studies of radio-tagged *Mustela*, although discussions of such difficulties are seldom published.

Problems with collars precipitated evaluations of intraperitoneal and subcutaneous implants for black-footed ferrets. Surgically implanted transmitters have been used effectively in several other mustelids such as river otters (*Lutra canadensis*; Hoover, 1984), badgers (Minta, 1993; Goodrich and Buskirk, 1998), and American mink (*Mustela vison*; Stevens and others, 1997). In 1985, we solicited prototype implantable transmitters suitable for ferrets from radio-telemetry equipment suppliers. Two of these units were designed for intraperitoneal use (table 1, versions D-5 and E-2), and a smaller unit (table 1, version D-4) was to be used subcutaneously. All had disappointingly low power output, leading us to believe that the problems we had in 1991 with loss of contact with ferrets would be worse with the implanted transmitters. Power output of the implants was initially lower than even that of the first radio collars used (table 1) and could be expected to be further degraded after implanting by signal attenuation caused by the ferret's body. Thus, we did not proceed to the next planned step in tests, which was to surgically implant the transmitters into surrogate Siberian polecats.

We did, however, use intraperitoneal and subcutaneous implants in American badgers at the Meeteetse study area in 1984. The dorsally implanted subcutaneous units with 15.2-cm implanted whip antennas radiated more powerful signals than did intraperitoneal units in the same animals, but abscesses that developed around the subcutaneous transmitters resulted in their premature loss. Compared to signals from the radio-tagged ferrets, which were then carrying relatively powerful transmitters (table 1, version D-1), signals from the subcutaneous implants in badgers were about as easily received from our fixed stations, but the intraperitoneal implants in badgers were much more difficult to track. Allowing that technology might have improved during the subsequent decade, we repeated the process of acquiring prototype implantable transmitters for ferrets in 1997, with generally similar results. Relatively poor reception range is a well-known attribute of implantable transmitters, in part because of the compromises necessary with transmitter antennas, which can translate into reduced precision and accuracy of data (Koehler and others, 2001). In our case, low power output resulted in rejection of implant technology before it was necessary to weigh the additional risks and costs of the surgeries needed for implanting and removing the transmitter. It also would have been necessary to consider the possible impact of implants on fertility of females and the possibility that implanted ferrets might not be locatable when it was time to remove the transmitter.

Radio-tracking Strategies

We quickly realized after radio tagging the first black-footed ferret in 1981 that signal-following techniques using hand-held tracking equipment were unlikely to generate the type, quality, and volume of data we were seeking. Much time was wasted searching for the subjects given the combination of relatively inefficient receiving antennas and low power output from the transmitters. Aside from the partial solution of developing more powerful transmitters (discussed above), it also was necessary to use much more directional and sensitive receiving antennas in order to maintain contact with the ferrets. Also, our signal-following attempts at night often appeared to disturb the ferrets. Thus, we decided to develop several stations of varying mobility equipped with larger antenna arrays from which tracking could be remotely accomplished via triangulation. Camper trailers with dual-beam 11- or 12-element, rotatable Yagi antennas (fig. 13) became the mainstay of the tracking system, augmented by more mobile truck-mounted receiving equipment (fig. 14). The relatively high receiving efficiency of these stations resulting from the larger antennas was further enhanced by increasing the heights of the arrays with masts of 4.5–6.0 m and by placing the stations on hilltops whenever possible. Although reception range was highly variable for these stations and the transmitters that were developed later (table 1, version D-3), we commonly radio-tracked ferrets at distances of 0.5–2.0 km and received signals from as far as 26.0 km on occasion (Biggins and others, 1999).

Knowing the exact locations of stations is a prerequisite for accurate triangulation. These data were produced (in Universal Transverse Mercator coordinates) by using traditional survey techniques (transit and chain) in the 1980s, followed by location data from a differentially corrected Global Positioning System in later years. Meticulous accuracy testing of each station improved the data in two ways. First, such tests allowed assessment of bias patterns inherent in each station and development of correcting algorithms to improve accuracy of data during processing. Second, the residual variation in bearings from stations, after bias was corrected, allowed estimates of accuracy to be associated with each estimated location for a ferret. Tests were conducted by contrasting telemetric bearings to 60–100 beacon transmitter locations surrounding the tested station with a set of known bearings to those beacon locations measured with a surveyor's transit (fig. 15). We employed a split sample technique to analyze test data, using half of the sample to derive the bias corrections and the second half to assess residual variation after the corrections were applied (fig. 16).

Figure 14. Truck-mounted, collapsible, 5-element Yagi array used to radio track black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyo., during 1982–84. Photograph by D. Biggins.

Figure 13. Camper trailer fitted with rotatable, 11-element, dual-beam Yagi array, used to radio track black-footed ferrets (*Mustela nigripes*) at the Meeteetse, Wyo., study area in 1983–84. Photograph by D. Biggins.

A second prerequisite for accurate triangulation is the ability to reference bearings from the antenna. Bearings can be usefully processed only when they are relative to a known

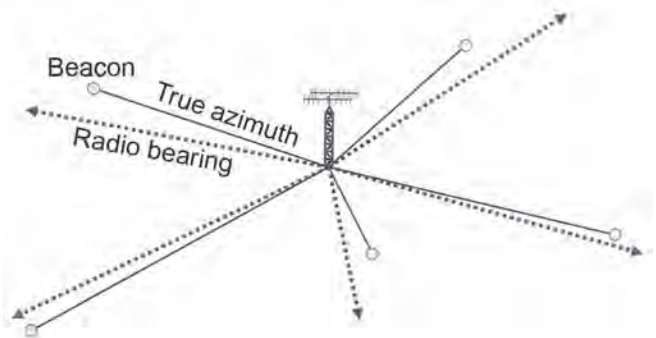

Figure 15. Accuracy testing and referencing involve comparison of true azimuths and radio bearings to beacon transmitters.

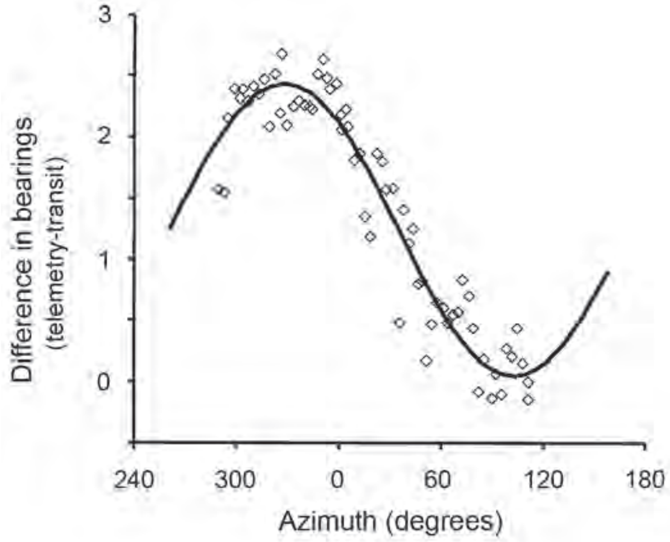

Figure 16. An accuracy test done at station 4, UL Bend National Wildlife Refuge, Mont., 1994. In this case, bias was corrected by using a formula defining the sine curve plotted. Residual variation produced a bias-adjusted accuracy estimate of ±0.63° (90% confidence) for future bearings from this station.

entity, such as grid north. One could simply align the main beam of the antenna to north with a compass and set the compass rose to zero. This method is rather crude (White and Garrott, 1990); at least two problems cause variable results. First, the physical and electronic alignment of antennas is seldom absolutely parallel. Second, there is considerable variation in the electronic aiming (fig. 16). If one could successfully get the aim exactly right at one particular point on the compass rose, then it would still not be correct for many other points around the compass rose. Some sort of averaging is needed. To solve these problems, we used reference transmitters placed at known points in the study area. Actual azimuths to the beacons were known for each station and were compared to the telemetric bearings to those transmitters (fig. 15), taken at the beginning of each tracking session. The compass rose inside a station was set so that zero was approximately at grid north (e.g., using a compass), and then readings to multiple beacons were used to provide an average correction that was applied to each subsequent bearing on an animal. Bias adjustment was applied before the referencing correction was made, the same as the process used when animals were tracked. Because the accuracy of this procedure affects all subsequent data, we cannot overemphasize the care needed in referencing. It would be nice to have many beacon transmitters (e.g., 50)! In practice, we used three to six beacons to avoid allowing referencing to become the dominant feature of a tracking session.

Although it is possible to plot triangulation data from pairs of these stations directly on maps to ascertain the whereabouts of the ferrets being tracked, it is more accurate and faster to process these data via computer. Advantages of conducting at least some of this processing while radio tracking include the following: (1) station selection can be adjusted as animals being tracked move about; (2) radio-tracking errors can be detected in time to correct them; (3) instances of mortality can be recognized quickly, resulting in better diagnoses of causes; (4) ferret dispersal can be detected in time to allow remedial action, if desired; and (5) in the case of lost radio contact, the last location calculated gives a starting point for searches. A computer program written by one of us (DEB) to accomplish these field processing tasks assisted the technicians with radio tracking ferrets at Meeteetse. The program was used on a programmable calculator in 1982 and was adapted to the first laptop computers that became widely available in 1983. That program evolved into TRITEL (Biggins and others, 2000b), which has been repeatedly modified since 1983 to accomplish referencing and bias corrections, convert azimuth data into coordinates, calculate error estimates for each telemetric fix (fig. 17), and store resulting data.

Procedures for radio tracking and processing data are detailed in a separate report (Biggins and others, 2000b). We have relied on intensive triangulation from these kinds of stations to produce large volumes of data. Although we have at times recollared ferrets to extend data gathering over several months, all telemetric studies were relatively short term. To monitor reintroductions, ferrets often were radio tracked for just 2–4 weeks postrelease, but stations were usually occupied during all hours of the day or during all hours of darkness, with fixes generated by occupants at two or more stations coordinating their tracking with two-way radio communication. Intensity of re-location for individual ferrets varied (3–60 minutes between consecutive fixes on an individual), depending mostly on how many individual animals were being monitored. During the reintroduction phase of black-footed ferret recovery (1989–2000), we used this tracking strategy

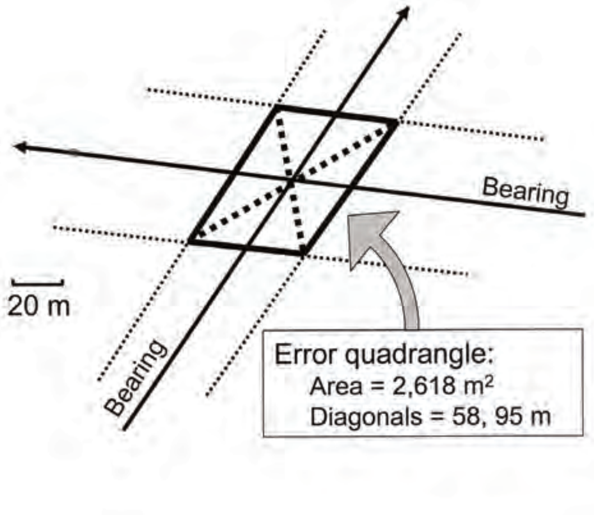

Figure 17. An example of a telemetric fix and error quadrangle (black-footed ferret [*Mustela nigripes*] no. 26, South Dakota, 10/23/97, 0148 h) produced by intersecting bearings and their associated error arcs from two tracking stations.

to monitor 340 radio-tagged ferrets and polecats, accumulating 83,275 lines of data that included 44,191 indications of status and 39,084 estimates of location (fixes). Data on status demarked beginning and ending points of tracking sessions, activity of animal (active, inactive) as determined by variation in signal strength, and pulse interval records when transmitters with variable pulse rates were used. Status data were recorded with fixes but were the only data recorded when triangulation was not possible (e.g., when only a single station received an adequate signal).

Radio-telemetry data from triangulation allows many options for analyses (summarized by White and Garrott, 1990). For black-footed ferrets, we have used radio telemetry to examine survival rates (Biggins, 2000a), linear movements (Biggins and others, 1999), dispersal (Biggins, Godbey, Livieri, and others, this volume), habitat preferences (Biggins and others, 1985; Biggins, Godbey, Matchett, and Livieri, this volume), indices of spatial use (Biggins and others, 1998b), and activity cycles (Biggins and others, 1986; Biggins, 2000a). The examples noted above are not exhaustive, and other options for use of the large data sets generated during multiple studies are currently being pursued. We believe that several features of analyzing telemetric data for ferrets, however, are worthy of emphasis here.

First, the inevitable errors that occur during triangulation must be detected and eliminated to the extent possible. Our system for handling data from triangulation, consistent with a pattern noted by Kenward (1987), has resulted in a series of custom computer programs for manipulating the output from TRITEL and screening for errors (Breck and Biggins, 1997). Similar to the BIOCHECK routine of White and Garrott (1990), our error screening involves searches for nonsensical data entries (e.g., unreasonable dates or times) and for data that fall outside limits set by a priori knowledge of ferret behaviors (e.g., maximum speed of movement). Errors are either corrected by referral to original data sheets, or offending lines are removed.

Second, estimates of ferret locations derived from triangulation are subject to direction-finding variation, as noted above. Estimates of such error associated with each fix ("error quadrangles" when two stations are used) are stored with each fix when TRITEL is used to process bearings. Our error screening process removes data lines with error estimates exceeding specified limits for lengths of diagonals or area of the quadrangle. Just as importantly, we have used these attributes of error as covariates in multivariate statistical analyses and often retain them in statistical models as "control" variables even if their estimated effect is small or not statistically significant. Although tracking error is nuisance variation when one is attempting to assess other treatments, it often accounts for significant variation (Biggins and others, 1998b, 2000a; Biggins, 2000a). If, however, a response variable is already known to be positively correlated to tracking error, then the use of tracking error as a covariate is not warranted. An example is dispersal. Because error is in part a function of distance separating station and subject, sizes of the error quadrangles increase as ferrets disperse away from tracking stations. Unlike other movements within the monitored area, radio-tracking error should not be used to explain variation in dispersal by ferrets because increased tracking error is an expected consequence of dispersal.

Third, the ferret data we have generated are serially correlated because of short interfix intervals; each telemetric fix cannot be considered independent (Swihart and Slade, 1985). The level of detail present in our data sets allows powerful behavioral comparisons (see examples cited above), but caution must be exercised in analyzing these data when independent observations are required (e.g., home range estimation; see White and Garrott, 1990).

The close association between black-footed ferrets and prairie dog colonies facilitates the radio tracking of ferrets from fixed tracking stations. Ferrets often remain within predictable boundaries where radio tracking coverage was nearly complete with careful placement of multiple stations (e.g., the Montana study of Biggins, Godbey, Matchett, and Livieri, this volume). Nevertheless, if we would like to monitor every animal in our sample with equal intensity and accuracy, triangulation from fixed stations is problematic (not unlike data from any other method of radio tracking or monitoring). Signal quality and accuracy of fixes vary with range and topography, and positioning of stations interacts with these factors to create uneven trackability of animals throughout any study area. The movements of some animals may be described more accurately and completely than the movements of others, and probabilities of detecting mortality cases may vary accordingly. Animals that disperse away from fixed stations may be tracked with lower intensity, lower accuracy, or not at all. Attributes such as cumulative movements are affected by frequency and accuracy of relocations. The consequences can be serious if the goal is to characterize the behaviors of the species. When comparing treatment groups (e.g., sexes, ages, rearing treatments), the consequences are more benign if we can reasonably assume that animals are distributed in the study area in such a way that members of each group are about equally trackable on average. The possibility of group-specific biases should be carefully considered for each case. For example, if dispersal is the attribute of interest, it may or may not be logical to rely on data from fixed-station triangulation. If dispersal distances have been artificially truncated by reception range of the tracking system, power of a comparative experiment may be reduced and dispersal distances will be underestimated to the greatest degree for groups whose members tend to disperse most frequently and farthest. Nevertheless, radio tracking from fixed stations has enabled us to detect significant between-group differences in dispersal (Biggins and others, 1998b, 1999). A germane statistical adage might be "if the tree falls, the axe was sharp enough" (Martin and Bateson, 1990, p. 126).

We have augmented triangulation with hand tracking, automated signal monitoring and data logging, and tracking from aircraft. Hand tracking, usually with a hand-held receiver and a 3-element Yagi antenna, was often used to investigate ferrets whose transmitters (a) were in unusual locations, (b) had moved rapidly, (c) had not been detected for long periods, (d) were stationary above ground at night, or (e) were above ground during daytime. These circumstances often led to re-location of ferrets that had dispersed (fig. 18) or to ferrets that had been killed by predators (fig. 19; Biggins, Godbey, Livieri, and others, this volume). We attempted to visit the location of the last fix if contact with a transmitter was lost for 2 or more days; listening for a radio signal while walking a narrowly spaced grid (ca. 2-m spacing) sometimes allowed detection of the transmitter belowground to depths of >4 m. Signal strength was correlated with depth of the transmitter; weakest signals could be received only when the operator was almost directly above the transmitter with the Yagi antenna pointing vertically downward (Biggins, 2000a). Signals seldom emanated from burrow entrances (contrary to the predictions of some electronic engineers). Remains of badger-killed ferrets were located by careful searches and excavated (fig. 20). Lost contact with transmitters also precipitated aerial searches at some sites. Each aircraft was equipped with a pair of 4-element Yagi antennas (affixed to each wing strut) and a switch to allow the operator to listen to the signal from each antenna separately. Homing on the source of a signal was accomplished by equalizing the null from each antenna (Gilmer and others, 1981). Radio-tracking flights helped locate ferrets that dispersed to different prairie dog colonies, especially when the flights were at night when ferrets are

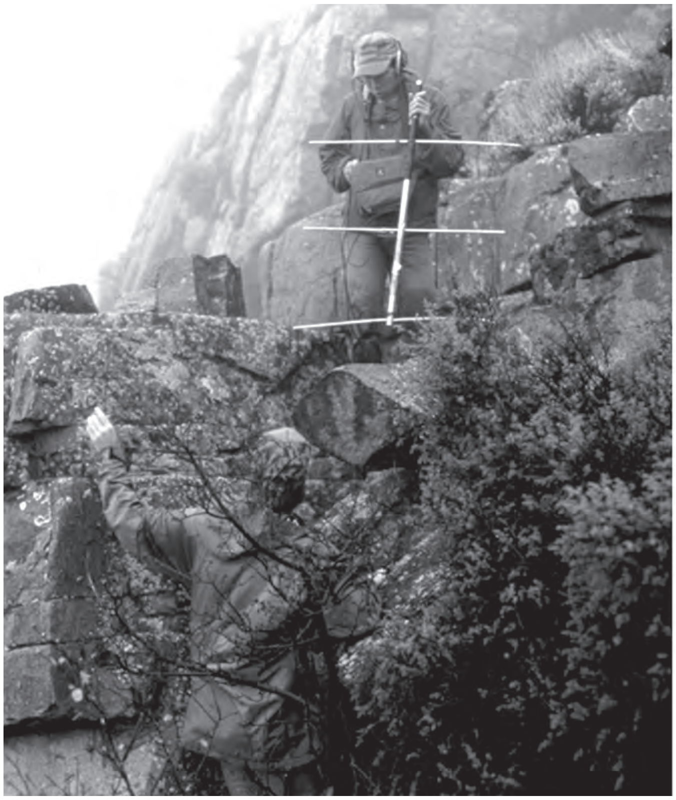

Figure 18. Hand tracking enabled us to locate black-footed ferrets (*Mustela nigripes*) that had dispersed into unusual habitats. Photograph by M. Albee.

Figure 19. Siberian polecat (*Mustela eversmannii*) killed by a predator. Photograph by D. Biggins.

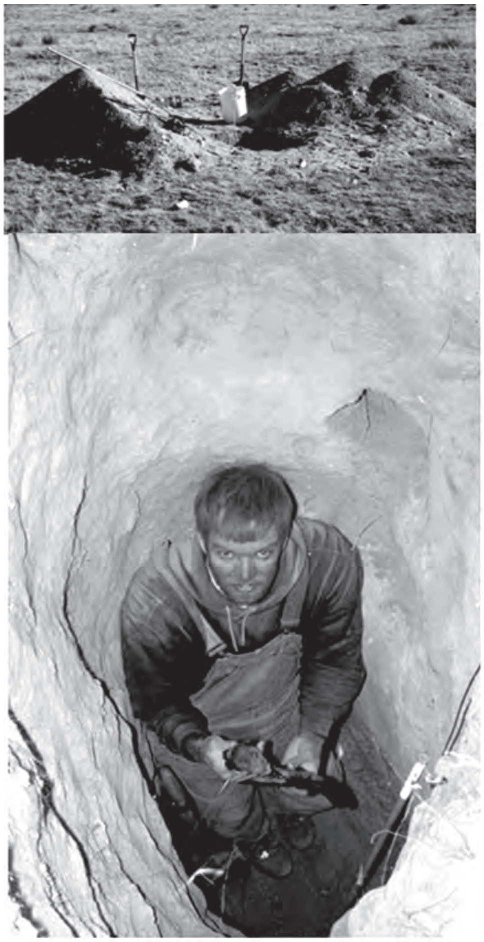

Figure 20. Hand-held tracking equipment enabled location of transmitters below ground, necessitating excavation to determine fate of animals such as this Siberian polecat (*Mustela eversmannii*) killed by a badger (*Taxidea taxus*). Photographs by D. Biggins.

most active above ground (Biggins and others, 1986; Biggins, 2000a). The most common product of flights, however, was detection of lost collars and cases of aboveground predation on ferrets that had dispersed (or their transmitters had been dispersed by the predator) beyond signal reception range of tracking stations. In short, these follow-up techniques, although arguably less technologically demanding than the radio tracking by triangulation, have provided the critically important details on fates of animals that other strategies cannot produce.

We used signal monitoring both with automated chart recorders and with computer loggers in attempts to collect information on aboveground activity of ferrets and polecats (Biggins, 2000a). The technique was useful to supplement data from triangulation, particularly on animals that were beyond the boundaries of the area that could be effectively monitored by tracking stations; however, the relative insensitivity of automated systems to detection of weak signals, coupled with the large activity areas of black-footed ferrets, limits the utility of automated tracking for ferrets.

Summary

The wide range of problems and accomplishments accompanying the use of radio telemetry on ferrets provides an opportunity for both detractors and proponents to present powerful arguments. Although success was never close to total, failures were not devastating to data or the ferrets. We would like to reemphasize that radio telemetry is an expensive and labor-intensive method for monitoring black-footed ferrets and that attaching radio transmitters to ferrets poses risks to the animals. It is essential, therefore, to carefully consider the objectives of a study to ascertain whether other tools would suffice. Justifications for use of radio telemetry on ferrets include unexplained lack of success in establishing a ferret population and tests of hypotheses that have large-scale management implications and require behavioral information. Cost/benefit analyses regarding use of telemetry should include as costs the potential future losses of ferrets if a perceived need for information remains unfulfilled. In some cases, short-term recovery objectives may become subordinate to learning objectives that could advance long-term recovery goals.

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References Cited

Biggins, D.E., 2000a, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., 2000b, Dispersal of radio-tagged black-footed ferrets released on prairie dog colonies in Wyoming, Montana, and South Dakota [abs.], *in* Proceedings of the 2000 Annual Meeting: Vernal, Utah Chapter of the Wildlife Society.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998a, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Godbey, J.L., Horton, B., and Livieri, T.M., 2000a, Experimental translocation of wild-born black-footed ferrets in South Dakota: Fort Collins, Colo., Fort Collins Science Center, U.S. Geological Survey, 14 p.

Biggins, D.E., Godbey, J.L., and Matchett, M.R., 1998b, Behavior and survival of black-footed ferrets (*Mustela nigripes*) when captive-born young were released into a free-ranging population: Fort Collins, Colo., Fort Collins Science Center, U.S. Geological Survey, 25 p.

Biggins, D.E., Hanebury, L.R., Godbey, J.L., and Miller, B.J., 2000b, Radio-triangulation and program TRITEL for wildlife research—an instruction manual: Fort Collins, Colo., Fort Collins Science Center, U.S. Geological Survey, 57 p.

Biggins, D.E., Schroeder, M., Forrest, S., and Richardson, L., 1985, Movements and habitat relationships of radio-tagged black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 11.1–11.17.

Biggins, D.E., Schroeder, M.H., Forrest, S.C., and Richardson, L., 1986, Activity of radio-tagged black-footed ferrets: Great Basin Naturalist Memoirs No. 8, p. 135–140.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Breck, S.W., and Biggins, D.E., 1997, Detecting and eliminating errors in radio-telemetry data sets—a comparison of screened and unscreened data [abs.], *in* Forum on wildlife telemetry—innovations, evaluations, and research needs: Jamestown, N. Dak., Northern Prairie Wildlife Research Center, U.S. Geological Survey, p. 15.

Byrom, A.E., 2002, Dispersal and survival of juvenile feral ferrets *Mustela furo* in New Zealand: Journal of Applied Ecology, v. 39, p. 67–78.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Erickson, R.C., 1973, Some black-footed ferret research needs, *in* Linder, R.L., and Hillman, C.N., preparers, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, p. 153–164.

Erlinge, S., 1979, Movements and daily activity pattern of radio tracked male stoats (*Mustela erminea*), *in* Amlaner, C.J., and Macdonald, D.W., eds., A handbook on biotelemetry and radio tracking: Oxford, U.K., Pergamon Press, p. 703–710.

Fagerstone, K.A., and Biggins, D.E., 1986, Summary of black-footed ferret and prairie dog research conducted by the Denver Wildlife Research Center, 1981–1985: Denver, Colo., Denver Wildlife Research Center, U.S. Fish and Wildlife Service, 31 p.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Gaynor, J.S., Wimsatt, J., Mallinckrodt, C., and Biggins, D., 1997, A comparison of sevoflurane and isoflurane for short-term anesthesia in polecats: Journal of Zoo and Wildlife Medicine, v. 28, p. 274–279.

Gilmer, D.S., Cowardin, L.M., Duval, R.L., Mechlin, L.M., Shaiffer, C.W., and Kuchle, F.B., 1981, Procedures for the use of aircraft in wildlife telemetry studies: U.S. Department of the Interior, Fish and Wildlife Service Resource Publication 140, 19 p.

Goodrich, J.M., and Buskirk, S.W., 1998, Spacing and ecology of North American badgers (*Taxidea taxus*) in a prairie-dog (*Cynomys leucurus*) complex: Journal of Mammalogy, v. 79, p. 171–179.

Hoover, J.P., 1984, Surgical implantation of radiotelemetry devices in American river otters: Journal of the American Veterinary Medical Association, v. 185, p. 1317–1320.

Jedrzejewski, W., Jedrzejewska, B., Zub, K., and Nowakowski, W.K., 2000, Activity patterns of radio-tracked weasels *Mustela nivalis* in Bialowieza National Park (Poland): Annales Zoologici Fennci, v. 37, p. 161–168.

Kenward, R.E., 1987, Wildlife radio tagging: San Diego, Calif., Academic Press, 222 p.

Kimmich, H.P., 1979, Artifact free measurement of biological parameters—biotelemetry, a historical review and layout of modern developments, *in* Amlaner, C.J., and Macdonald, D.W., eds., A handbook on biotelemetry and radio tracking: Oxford, U.K., Pergamon Press, p. 3–20.

Koehler, G.M., Hall, P.B., Norton, M.H., and Pierce, D.J., 2001, Implant- versus collar-transmitter use on black bears: Wildlife Society Bulletin, v. 29 p. 600–605.

Linder, R.L., and Hillman, C.N., preparers, 1973, Proceedings of the black-footed ferret and prairie dog workshop: Brookings, South Dakota State University, 208 p.

Marcelli, M., Fusillo, R., and Boitani, L., 2003, Sexual segregation in the activity patterns of European polecats (*Mustela putorius*): Journal of the Zoological Society of London, v. 261, p. 249–255.

Martin, P., and Bateson, P., 1990, Measuring behaviour, an introductory guide: Cambridge, U.K., Cambridge University Press, 200 p.

Miller, B., Reading, R.P., and Forrest, S., 1996, Prairie night—black-footed ferrets and the recovery of endangered species: Washington, D.C., Smithsonian Institution Press, 254 p.

Minta, S.C., 1993, Sexual differences in spatio-temporal interaction among badgers: Oecologia, v. 96, p. 402–409.

Moller, H., and Alterio, N., 1999, Home range and spatial organization of stoats (*Mustela erminea*), ferrets (*Mustela furo*) and feral house cats (*Felis catus*) on coastal grasslands, Otago Peninsula, New Zealand—implications for yellow-eyed penguin (*Megadyptes antipodes*) conservation: New Zealand Journal of Zoology, v. 26, p. 165–174.

Oakleaf, B., Luce, B., and Hnilicka, P., 1993, Survival and dispersal of captive raised black-footed ferrets reintroduced in Shirley Basin, Wyoming. A comparison between black-footed ferrets released with and without telemetry collars, *in* Oakleaf, B., Luce, B., Thorne, E.T., and Williams, B., eds., Black-footed ferret reintroduction in Shirley Basin, Wyoming, 1992, Annual Completion Report: Cheyenne, Wyoming Game and Fish Department, p. 188–219.

Stevens, R.T., Ashwood, T.L., and Sleeman, J.M., 1997, Fall–early winter home ranges, movements, and den use of male mink, *Mustela vison*, in eastern Tennessee: Canadian Field-Naturalist, v. 111, p. 312–314.

Swihart, R.K., and Slade, N.A., 1985, Testing for independence of observations in animal movements: Ecology, v. 66, p. 1176–1184.

Thorne, E.T., Schroeder, M.H., Forrest, S.C., Campbell, T.M., III, Richardson, L., Biggins, D., Hanebury, L.R., Belitsky, D., and Williams, E.S., 1985, Capture, immobilization, and care of black-footed ferrets for research, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 9.1–9.8.

Ubico, S.R., Maupin, G.O., Fagerstone, K.A., and McLean, R.G., 1988, A plague epizootic in the white-tailed prairie dogs (*Cynomys leucurus*) of Meeteetse, Wyoming: Journal of Wildlife Diseases, v. 24, p. 399–406.

U.S. Fish and Wildlife Service, 1992, Reintroduction of the black-footed ferret (*Mustela nigripes*): Fort Collins, Colo., National Ecology Research Center, 44 p.

Wei, W., Zhou, W., Fan, N., and Biggins, D., 1996, Activity rhythm and home range of the alpine weasel (*Mustela altaica*): Acta Theriologica Sinica, v. 16, p. 35–42.

White, G.C., 1983, Numerical estimation of survival rates from band-recovery and biotelemetry data: Journal of Wildlife Management, v. 47, p. 716–728.

White, G.C., and Garrott, R.A., 1990, Analysis of wildlife radio-tracking data: San Diego, Calif., Academic Press, 383 p.

Zabala, J., Zuberogoitia, I., Garin, I., and Aihartza, J., 2003, Landscape features in the habitat selection of European mink (*Mustela lutreola*) in south-western Europe: Journal of the Zoological Society of London, v. 260, p. 415–421.

Zhou, W., Wei, W., and Biggins, D.E., 1994, Activity rhythms of polecats (*Mustela eversmannii*) in the Qing-Zang Plateau: Acta Biologica Plateau Sinica, v. 12, p. 173–187.

Appendix. Notes on Radio Collaring Black-footed Ferrets

Collars that we are presently using are considerably more fragile than their predecessors and are intentionally designed to lack durability. Most black-footed ferrets (*Mustela nigripes*) shed the collars within 2 months (often much sooner). Use of more durable collars seems to increase the risk of neck sores. Presently, collars 1 cm wide are made of 100 percent wool, folded into three layers and sewn with 100 percent cotton thread. The edges are not bound, so the wool will fray rapidly. After sewing the wool into long strips of uncut collars, we prestretch the material. It is soaked in water and hung to dry with a 200-g weight clamped to the lower end. Collars are then cut to 15–18 cm lengths. To attach a collar to the transmitter unit, both are inserted into a 2.5-cm length of Teflon® heat-shrink tubing (1.25 cm diameter), and a heat gun (or other heat source such as a gas stove or propane torch) is used to shrink the tubing. Overheating the transmitter packages can cause malfunctions. High temperature for a short duration works better than less heat applied for longer times. The object is to heat the tubing without overheating the transmitter and battery. After shrinking the tubing, the package is cooled rapidly by wrapping it in a cool, wet sponge. Equipment and supplies needed to attach these collars to ferrets include scissors, a hemostat clamp, contact cement, a telemetry receiver, and a hair dryer. Mustelids characteristically have little neck constriction, making exact collar fit important. The attachment procedure for black-footed ferrets may be accomplished in the following steps:

1. Remove the magnet and check transmitter operation.
2. Restrain ferrets with a light dose of ketamine/diazepam (about 17–20 mg per kg of body weight) for this noninvasive procedure (Thorne and others, 1985). Recently, we have been using isoflurane gas anesthesia, which is more controllable (Biggins, Godbey, Matchett, and others, this volume). New innovations in gas anesthesia (e.g., sevoflurane; Gaynor and others, 1997) have additional advantages but require different vaporizers. The U.S. Fish and Wildlife Service requires ferret handlers to be trained in anesthesia and handling procedures.
3. As soon as the animal is tranquil enough to handle, make a trial fit of the collar and mark the length needed, allowing about 1-cm overlap of ends. Mark the area of overlap that will be glued, but do not trim excess from the long end of the collar until later. The extra length makes it easier to fit on the animal and can be trimmed at the end of the process.
4. Coat the inside of one end and the outside of the other end with contact cement. We use the Weldwood® (DAP® Products, Inc., Baltimore, Md.) version that has a toluene solvent, which seems to work better than the versions with other solvents. The glue-drying process takes 3–10 minutes. A hair dryer speeds drying. The first coat of cement normally penetrates the wool. Unless the glue is quite thick, the first coat must be dried completely and a second coat applied and dried until tacky.
5. Wrap the collar around the animal's neck and press a tiny portion of the glued strip together lightly. This process allows a final check for snugness before the final gluing is done. Collar fit is critical; it should be snug but not tight. The collar should rotate fairly easily around the neck. Also, a small closed hemostat or small scissors should slide easily between the neck and collar, but if you can insert your little finger, the collar is probably too loose.
6. If the fit seems satisfactory, press the glued ends together firmly. Use the hemostat to clamp the ends, repeatedly clamping and releasing until the entire overlap area has been pressed together firmly. Trim excess wool from the long end of the collar. We know of only one occasion when the glue joint failed, and that was when a technician did not realize that he had to let the glue dry before pressing the ends together. In fact, we have not been able to separate the final joint by pulling the ends apart—the material always tears. It may even be difficult to separate the ends during the trial fitting if they have made too much contact.

Postrelease Movements and Survival of Adult and Young Black-footed Ferrets

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Abstract

A successful captive breeding program for highly endangered black-footed ferrets (*Mustela nigripes*) has resulted in surplus animals that have been released at multiple sites since 1991. Because reproductive output of captive ferrets declines after several years, many adult ferrets must be removed from captive breeding facilities annually to keep total production high. Adults are routinely released, with young-of-the-year, on prairie dog (*Cynomys* spp.) colonies. We evaluated postrelease movements and survival rates for 94 radio-tagged young and adult ferrets. Radio-tagged adult ferrets made longer movements than young ferrets during the night of release and had significantly lower survival rates for the first 14 days. Coyotes (*Canis latrans*) caused the largest number of ferret losses. A larger data set of 623 ferrets represented adults and young that were individually marked with passive integrated transponders but were not radio tagged. Minimum survival rates, calculated primarily from ferrets detected during spotlight searches and identified with tag readers, again were significantly lower for adults than for young ferrets at 30 days postrelease (10.1 percent and 45.5 percent survival, respectively) and at 150 days postrelease (5.7 percent and 25.9 percent). Assessment of known survival time by using linear modeling demonstrated a significant interaction between age and sex, with greater disparity between adults and kits for females than for males. Postrelease survival of adult ferrets might be increased if animals were given earlier and longer exposure to the quasi-natural environments of preconditioning pens.

Keywords: age, behavior, mortality, *Mustela nigripes*, predation, radio telemetry

Introduction

Black-footed ferrets (*Mustela nigripes*) nearly became extinct when diseases invaded the last known free-ranging population near Meeteetse, Wyo., in 1985 (Lockhart and others, this volume). A rescue effort resulted in a captive population that has provided ferrets for reintroduction since 1991. The mean life expectancy of free-ranging black-footed ferrets in the ancestral Meeteetse population was about 0.9 years (calculated by using the negative reciprocal of the natural log of 0.34, an annual survival rate estimated by Forrest and others, 1988). With such a short average life expectancy, natural selection may have applied little pressure for sustained productivity in older age classes of ferrets. In captivity, productivity declines rapidly after ferrets are only a few years old (Williams and others, 1991). Efficient management of the captive breeding program thus involves relatively rapid rotation of animals (Marinari and Kreeger, this volume). Older animals are placed in zoos for exhibit and used for research, but the supply of such animals exceeds the demand. Adult ferrets are routinely released at reintroduction sites, a practice that has been criticized. Although both young and adult ferrets have been released at several sites, their postrelease movements and survival have not been compared. Marking of animals, spotlight searches, and identification of surviving ferrets are tools routinely used for monitoring at release sites (Biggins, Godbey, Matchett, and others, this volume), providing useful multiyear data sets. In certain years, more intensive radio-telemetry studies (Biggins, Godbey, Miller, and Hanebury, this volume) were directed at testing hypotheses regarding prerelease experience and rearing methods. Cumulative data from these former efforts provide the opportunity to contrast the movements and survival of released adult and young ferrets.

Methods

Stratification Based on Rearing and Prerelease Experience

Rearing conditions and prerelease experience have profound effects on behaviors of young ferrets (Miller and

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others, 1990a,b; Vargas, 1994; Biggins and others, 1999; Biggins, 2000), ultimately influencing postrelease survival rates (Biggins and others, 1998). Released adult (age at release >1 year) black-footed ferrets reported herein were given experience in outdoor pens, including living in natural burrows and killing prairie dogs, for 1–4 months prior to release. Former experimental designs that focused on testing effects of rearing on young ferrets (kits), however, involved more categories of preconditioning and more carefully controlled environments (Biggins and others, 1998). Those experimental designs encompassed most of the radio-tagged kits used in the following analyses but only a portion of the released kits that were not telemetrically monitored. Because early experiments indicated that cage-reared kits were dramatically different in several respects from their counterparts with experience in pens (Biggins and others, 1998, 1999), we did not include cage-reared kits in any of our analyses (telemetry or recapture). We also excluded kits that were born in pens or transferred into pens at the natal facility at an early age (<60 days) with their dams (the PENRES category of Biggins and others, 1998) from the telemetric data set. For a large number of kits that were not part of the early experiments, preconditioning was much more variable. Thus, our capture-recapture analyses encompassed a more broadly defined “preconditioned” group of kits that ranged from those placed in pens prior to 60 days of age with dams to those shipped after 90 days of age, without accompanying adults, from their original breeding facility to pens at other facilities or to remote pens near reintroduction sites.

In summary, we used two types of data to examine the influence of age of ferrets on their movements and survival. Radio telemetry provided information on cumulative movements, dispersal, minimum survival rates, and causes of mortality. A larger sample of ferrets that were individually marked (including those that were radio tagged) allowed additional estimates of survival via mark-recapture methods.

Radio Telemetry

We radio collared 137 black-footed ferrets with 5-g transmitter packages attached to 100 percent wool collars with Teflon® (DuPont, Wilmington, Del.) heat-shrink tubing (the latter to resist mud accumulation). Radio-tagged ferrets were released on Gunnison’s prairie dog (*Cynomys gunnisoni*) habitat in the Aubrey Valley of northern Arizona and on black-tailed prairie dog (*C. ludovicianus*) habitat at UL Bend National Wildlife Refuge in Montana and the Burns Basin portion of Badlands National Park, S. Dak.

Transmitters, with their 20-cm whip antennas, provided a pulsed signal (pulse interval = 1.5 seconds; pulse width = 20 milliseconds) of about -14 dB, with battery life of about 45 days. Radio location was accomplished via triangulation from fixed stations fitted with paired, 11-element Yagi antennas on rotating masts (Biggins and others, 1999; Biggins, Godbey, Miller, and Hanebury, this volume). We tested accuracy of stations by comparing station-derived azimuths with true azimuths to beacon transmitters. We used standard deviations of the differences between such pairs in confidence intervals to predict the accuracy of future azimuths and the areas and diagonals of error quadrangles associated with positional “fixes” (White and Garrot, 1990). An initial test for each station provided data for evaluating bias patterns and developing formulas for adjustment, and a second set of readings was used to calculate residual variation after bearings were adjusted (Biggins and others, 1999). We referenced stations prior to each tracking session (Biggins, Godbey, Miller, and Hanebury, this volume) using from 2 to 5 beacon transmitters. For these analyses, we used radio-telemetry data for the first 14 days postrelease (although tracking extended over a longer period at some sites). We used the computer program TRITEL to process azimuth data (Biggins, Godbey, Miller, and Hanebury, this volume); processing included adjustments for referencing and bias and calculation of coordinates and error estimates for each fix. Hand-held tracking equipment assisted us in recovery of lost collars and dead ferrets.

For comparisons of age groups, we used the subset of the 137 instrumented animals (excluding 20 PENRES kits and 23 cage-reared kits as defined above) that included 38 adults and 56 “preconditioned” kits (table 1). We screened data for gross radio-tracking and data entry errors by using the systematic approach of Breck and Biggins (1997). We then summarized cumulative movements between consecutive fixes and dispersal from the release site for each ferret and night. We analyzed cumulative movements by using a repeated measures multivariate general linear model (MGLM) with average area of error quadrangle, sex, and site as covariates. We used square root transformations of the response variables to improve normality and homoscedasticity of residual variation. We assumed that the area of an error quadrangle would account for a portion of the variation in the cumulative movement of a ferret and retained this measure of tracking error as a control variable in statistical models regardless of its significance. Because dispersal is defined as movement away from the release site and increased distance from tracking stations causes larger error quadrangles, tracking error was not considered in statistical evaluations of dispersal, but sex and site were included as covariates.

Causes of mortality were determined by evidence at recovery sites (e.g., tracks, scat, fur, feathers, digging), condition of carcass (e.g., hemorrhage, bite wounds, saliva), and radio-tracking data (patterns of fixes and activity, timing of death). We assessed risk-adjusted survival rates by relating deaths (table 1) to days of telemetric monitoring (Heisey and Fuller, 1985). An estimate of maximum survival resulted from considering only known deaths. Counts of animals known dead underestimate mortality rates because not all dead animals are detectable (underground deaths due to badgers, for example, may be underestimated) and because some proportion of loss of telemetric contact with animals is due to transmitter damage inflicted during predation. (We have recovered a few badly damaged transmitters that were barely functional and assume that others became nonfunctional.) We thus

Table 1. Numbers of preconditioned adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) released in Arizona, South Dakota, and Montana during 1994–96.

	Arizona (1996)	South Dakota (1995–96)	Montana (1994)	Montana (1995)	Total
Ferrets					
Adult	15	14	5	4	38
Kit	8	11	10	27	56
Total	23	25	15	31	94
Ferret-days of monitoring					
Adult	90.7	21.3	25.0	29.7	166.7
Kit	43.0	93.2	54.0	291.0	481.2
Total	133.7	114.5	79.0	320.7	647.9
Deaths					
Adult	4	11	3	1	19
Kit	0	5	5	1	11
Total	4	16	8	2	30

estimated a minimum survival rate by summing the number of ferrets that were lost from telemetric contact and the number known to be dead. If an animal was found alive at a later date during spotlight surveys, it was considered alive for the first 14 days (even if telemetric contact was lost and it would have been listed as missing). If an animal died or became missing after 14 days, it was treated as alive for the first 14 days. Our multivariate general model had eight parameters (two ages, four site/year combinations). In this survival analysis, we compared models and their nested submodels using likelihood ratio tests.

Table 2. Numbers of preconditioned adult and young black-footed ferrets (*Mustela nigripes*) marked and released at sites in Montana, South Dakota, and Utah-Colorado during 1994–2001.

	South Dakota (1994–2000)	Montana (1994–97)	Utah-Colorado (1999–2001)	Total
Adult	49	13	60	122
Kit	261	80	160	501
Total	310	93	220	623

Mark-recapture

The data set for this portion of the study (table 2) included all black-footed ferrets released during 1994–2000 at Badlands National Park and Conata Basin in South Dakota, ferrets released during 1994–97 at UL Bend in Montana (including the radio-tagged individuals mentioned above), and ferrets released at the Coyote Basin site of Utah and adjacent Colorado. Of the 623 ferrets released (table 2), 325 were males and 298 were females. All released ferrets were individually marked, mostly with passive integrated transponder (PIT) tags subcutaneously implanted over the shoulder. A second PIT tag often was implanted over the hip (Biggins, Godbey, Matchett, and others, this volume). “Recapture” (in this case, mostly reading the transponder) was accomplished via spotlight surveys to locate the ferrets (Campbell and others, 1985; Biggins and others, 1998) followed by placement of a transponder reader at the occupied burrow to automatically read and retain the chip number (Biggins, Godbey, Matchett, and others, this volume). The first survey at each site usually was conducted about 1 month postrelease, with additional surveys conducted prior to the breeding season (in some cases) and postwhelping (most sites). Intensity of these survey efforts varied among sites and years due to availability of resources.

Counts of surviving animals at 30 and 150 days postrelease were based on the same released ferrets and thus cannot be considered statistically independent. Also, the 71 radio-tagged ferrets in South Dakota and Montana are a subset of the 623 animals considered in the capture-recapture analyses. We chose to maintain separate 30-day and 150-day mark-recapture analyses (rather than a more complex single model) because of sample size differences and unequal time intervals between surveys and because survival estimates for these time periods can be compared with similar estimates reported elsewhere for ferrets. Survival was considered cumulatively; ferrets found alive at 150 days (or later) were counted as alive on day 30 even if they were not found in the earlier period. Because spotlight sessions of equal intensity were not replicated systematically at all sites (or even among days within sites), we did not attempt traditional capture-recapture modeling where capture rates and survival rates could be estimated separately. Our rates, therefore, must be considered as minimum survival (the products of capture rate and survival rate), recognizing that not all ferrets were likely to have been located at any site. Interpretation of the comparisons between adults and kits thus requires the assumption that each age class (within each site) was equally detectable by spotlighting, an assumption that we believe is reasonable. We estimated survival rates from spotlight searches by using an iterative numerical optimization procedure (program SURVIV; White, 1983). The general model included 12 parameters (3 sites, 2 sexes, 2 ages).

Elapsed time from release until the last detection for each ferret also was calculated. Time intervals between releases and the first spotlight survey and between subsequent spotlight surveys varied considerably among sites and years, from a single survey per year to nearly continuous surveys. Variability in survey timing tended to distribute this measure of survival in a continuous (but skewed) form, and square root transformation improved its suitability for use as a continuous response variable in a MGLM analysis, allowing additional assessment of the potential interaction between age and sex.

We recognize that detectability of ferrets via spotlight searches is likely to differ among sites due to differences in access, vegetative cover, topography, intensity of effort, and other variables. Thus, we consider multivariate modeling, with a site variable included, as critically important. Potential differences in search efficiency also preclude any conclusions regarding differences in survival among sites.

An important consideration in our experimental design, for both telemetric and capture-recapture data, was to maintain a reasonable balance of treatments within sites (and within years, with one exception). Other priorities always affected allocations of animals, but, to avoid serious confounding during interpretation of results, we did not allow any cell of the design to be empty. Thus, groups of released ferrets that did not contain adults and kits of both sexes were excluded from analyses. The exception to this general rule occurred within the telemetry data set, where adult ferrets were released in Badlands National Park in spring, and kits were released at that site during fall of the following year.

We followed the principle of parsimony in evaluating competing statistical models (Lebreton and others, 1992), attempting to reduce general models to simpler submodels by eliminating variables that appeared to have low explanatory power. For capture-recapture analysis within program SURVIV, reduced models were evaluated by likelihood ratio tests and Akaike's Information Criterion (AIC) (Anderson and Burnham, 1994). For MGLM evaluations and likelihood ratio testing, P values >0.10 were deemed sufficient for eliminating variables from models.

Results

Radio Telemetry

Of the 137 radio-tagged ferrets that were released, 59 were considered lost to the population, mostly as a result of predation (fig. 1). Coyotes (*Canis latrans*) caused the most losses, but prior to its removal a great horned owl (*Bubo virginianus*) had a substantial impact at one site in South Dakota. American badgers (*Taxidea taxus*) were common on prairie dog colonies where ferrets were released, but they killed ferrets only occasionally. The species of predator responsible for ferret deaths could not always be determined, however, resulting in some classifications of "unknown predator" or "unknown raptor" (fig. 1).

Multivariate repeated measures analysis of square root transformed cumulative movements for ferrets that were monitored for at least three nights yielded a significant interaction between night postrelease and age group ($F_{2,59} = 7.407$, $P = 0.001$) with a model that included age, site, and mean area of error quadrangle (per animal over three nights). Thus, the pattern of change in nightly movements of kits and adults was significantly different over the first three nights postrelease (fig. 2; nontransformed data). Tracking error (area of error quadrangle) contributed significantly to the variation in movements ($F_{1,60} = 5.620$, $P = 0.021$), underscoring the importance of a variable to account for this source of "nuisance" variation

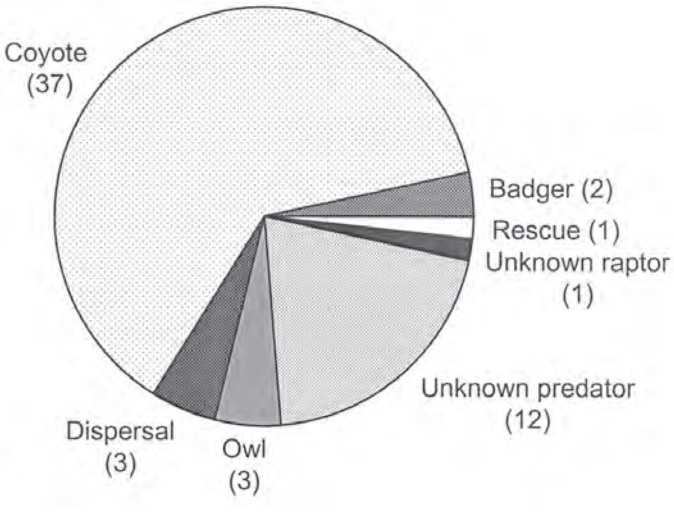

Figure 1. Causes of loss for 59 of 137 radio-tagged black-footed ferrets (*Mustela nigripes*) released in Montana, South Dakota, and Arizona during 1994–96. "Rescued" ferrets are those that we assume would have been lost without our intervention (translocation or treatment for injuries). "Unknown predator" and "Unknown raptor" are general categories for which the species of predator could not be identified.

in models of movement. Nightly movements also appeared to be different at different sites ($F_{3,60} = 3.693$, $P = 0.017$).

The relatively long movements of adult ferrets on the night of release suggested that they might have "bolted" from the release site (i.e., dispersed rapidly away from the point of release), but a repeated measures analysis of dispersal during the first three nights did not support that contention (fig. 3). Although there was a significant tendency for ferrets to drift away from their release sites over the first several nights ($F_{2,58} = 8.860$, $P < 0.001$), the pattern of dispersal was not significantly different for kits and adults ($F_{2,58} = 1.107$, $P = 0.337$). Thus, "bolting" is not an appropriate description of the behaviors of adults. They simply moved more than kits during their first night but did not tend to leave the area of release any differently than did kits. In this analysis of dispersal, there was no evidence of differences among sites ($F_{3,59} = 1.209$, $P = 0.315$).

Survival of radio-tagged adults appeared to differ significantly from survival of radio-tagged kits. For the estimates of maximum survival, generated by considering only known deaths (fig. 4), likelihood ratio testing did not support reduction in number of parameters by pooling sites ($X^2 = 45.4$, $df = 6$, $P < 0.001$) or ages ($X^2 = 29.3$, $df = 4$, $P < 0.001$). The same was true for the estimates of minimum survival, using ferrets known to be dead plus those with whom radio contact was lost during the 14-day tracking period (sites, $X^2 = 38.6$, $df = 6$, $P < 0.001$; ages, $X^2 = 38.7$, $df = 4$, $P < 0.001$). There was thus a similar overall pattern of differences between survival rates of adults and kits, regardless of the method of categorizing mortalities (fig. 5). If about one-third of the missing animals actually died when their signals were lost, the overall projected survival rates for 30 days postrelease would have been 42 percent for kits and 11 percent for adults. The curves vary among sites and with methods, but kit survival was higher than adult survival within each comparison.

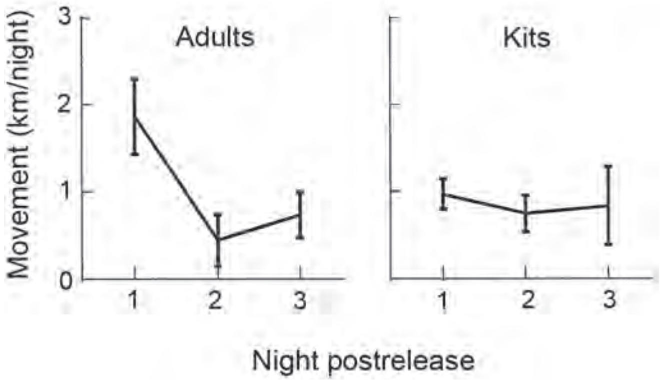

Figure 2. Mean cumulative nightly movements for adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) during the first three nights postrelease (mean ± SE).

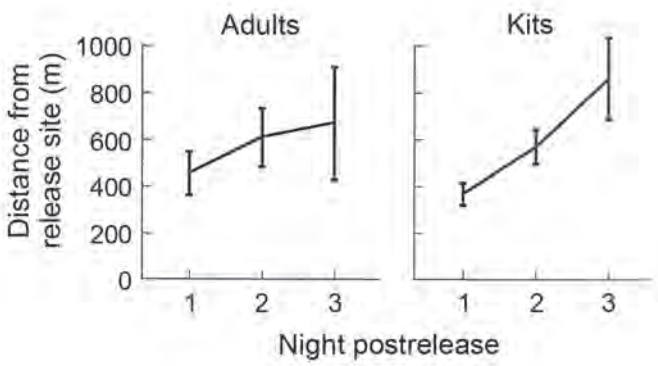

Figure 3. Nightly maximum displacement from release sites for young and adult radio-tagged black-footed ferrets (*Mustela nigripes*) during the first three nights postrelease (mean ± SE).

Mark-recapture

The preferred model of minimum survival from the spotlight search data was the general model for both the short-term (30-day) (table 3) and the long-term (150-day) assessment (table 4), although the evidence for distinction between the sexes was strongest in the long-term evaluation. Minimum survival rates were higher for kits than for adults in 11 of the 12 pairs of estimates for the two time periods, averaging 45.5 percent (kits) and 9.8 percent (adults) at 30 days (fig. 6) and 25.9 percent (kits) and 5.7 percent (adults) at 150 days (fig. 7). Minimum survival rates tended to be higher for females

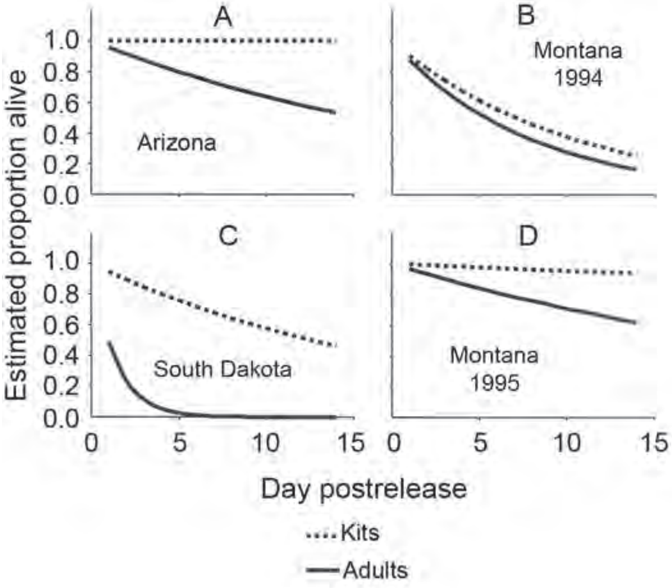

Figure 4. Postrelease survival curves for preconditioned adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) extrapolated from daily survival rates (assuming a constant hazard rate for the 14-day period of the experiment and using only known deaths).

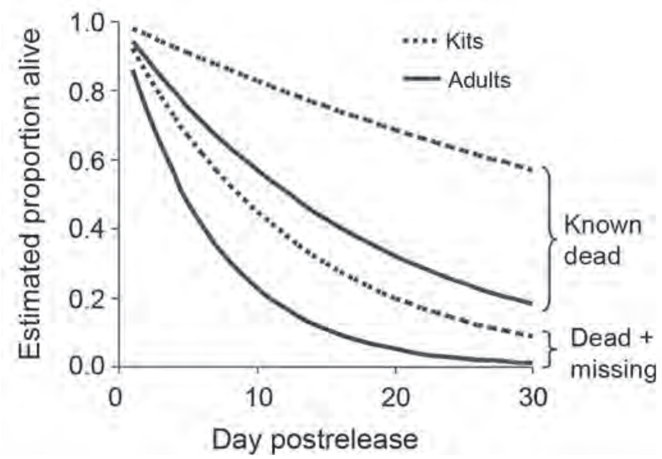

Figure 5. Bracketed high and low survival of adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) for the first 30 days postrelease, generated by using only ferrets known to be dead (high) and known deaths plus ferrets lost to radio contact (low). Curves were extrapolated from daily survival rate estimates assuming a constant hazard rate for the period.

than for males (figs. 6 and 7). For kits, the disparity between sex-specific survival rates was proportionately greater for the long-term estimates (males, 18.9 percent; females, 35.7 percent) than for the short-term estimates (males, 39.9 percent; females, 53.4 percent). Moreover, there seemed to be different patterns for adults and kits within the two genders for both the short-term and long-term data sets. That potential interaction warranted closer examination.

General linear modeling of elapsed time between release and the last detection demonstrated a significant interaction between sex and age ($F_{1,617} = 5.522$, $P = 0.011$); known survival times tended to be shorter for adults than for kits (fig. 8). We retested the sexes separately because of the interaction. As implied by the pairs of graphs, female kits survived significantly longer than did adult females ($F_{1,294} = 40.250$, $P < 0.001$), but the difference between the age groups was only marginally significant for males ($F_{1,294} = 3.387$, $P = 0.067$).

Discussion

Radio Telemetry

There is a potential bias built into assessments of ferret movements. Repeated measures analyses, particularly, require complete sets of multiple measures on single animals; any ferret that lacked a measure of movement for any of the first three nights postrelease (fig. 2), for example, was excluded from our analysis. Thus, ferrets that tend to engage in risky behaviors tend to be removed (by death) at higher rates from the sample, likely causing movements to be generally underestimated, and (more seriously for this kind of experiment) the effect may be greater on some treatment groups than on others. If we assume that there is a positive correlation between movement and mortality rate (Biggins and others, 1998), we likely underestimate movement differences between groups. We have been able to detect such differences, but more subtle disparities between treatment groups may remain unnoticed. Statistical models that are not based on repeated measures also would be affected, but more flexible rules for handling those data should result in a less dramatic influence. Although early deaths of individuals having presumably lower fitness may cause a shift in representation of animals, their movements before they were killed remain in data sets used for statistical analyses other than repeated measures.

Survival of radio-tagged kits differed more dramatically from adults at the Burns Basin, S. Dak., release site than at any other site (fig. 4). Although the same release site was used for both kits and adults, and they were radio tracked from the same system, Burns Basin was the only site where adults and kits were not released at the same time. It is possible that the differences there were due to year or season.

The different appearance of survival curves among sites generated from telemetric data (fig. 4) should not be construed as being linked to the species of prairie dog or other site-specific conditions. Efficiency of radio tracking is likely responsible for much of the variation. The Aubrey Valley site

Table 3. Modeling of short-term (30-day) return rates for preconditioned black-footed ferrets (*Mustela nigripes*) released at three sites, with parameter estimates for sites, sexes, and ages.

Model	ln(L)[a]	np[b]	AIC[c]	Versus model[d]	X^2	P
1. General	-19.842	12	63.685			
2. Sites same	-65.391	4	138.783	1	91.10	<0.001
3. Ages same	-53.722	6	119.443	1	67.76	<0.001
4. Sexes same	-28.060	6	68.120	1	16.44	0.012

[a] ln(L) = log-likelihood.

[b] np = number of parameters.

[c] AIC = Akaike's Information Criterion.

[d] The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.

Table 4. Modeling of long-term (150-day) return rates for preconditioned black-footed ferrets (*Mustela nigripes*) released at three sites, with parameter estimates for sites, sexes, and ages.

Model	ln(L)[a]	np[b]	AIC[c]	Versus model[d]	X^2	*P*
1. General	-16.687	12	57.374			
2. Sites same	-34.662	4	77.324	1	35.95	<0.001
3. Ages same	-35.060	6	82.121	1	36.75	<0.001
4. Sexes same	-28.609	6	69.219	1	23.84	0.001

[a] ln(L) = log-likelihood.

[b] np = number of parameters.

[c] AIC = Akaike's Information Criterion.

[d] The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.

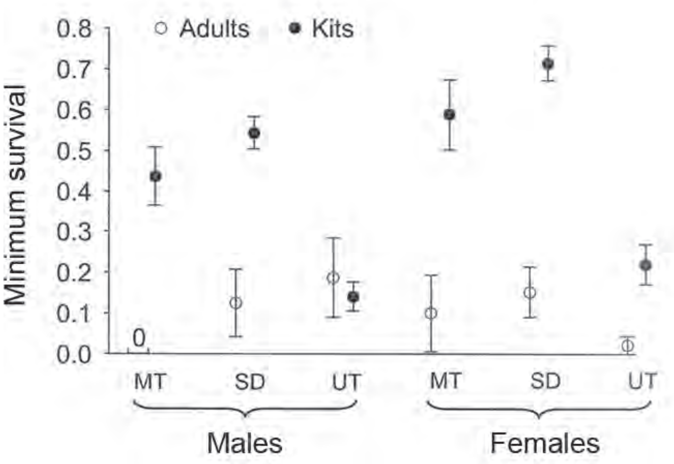

Figure 6. Minimum short-term (30-day) survival of adult and young preconditioned black-footed ferrets (*Mustela nigripes*) released onto prairie dog colonies (*Cynomys* spp.) in Montana (MT), South Dakota (SD), and Utah (UT) during 1994-2001 (mean ± SE).

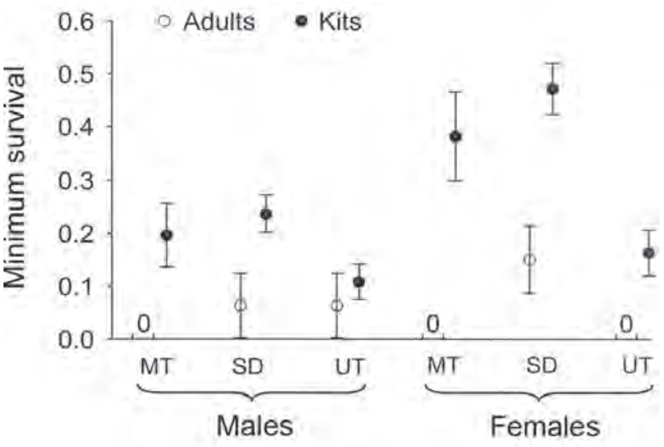

Figure 7. Minimum long-term (150-day) survival of adult and young preconditioned black-footed ferrets (*Mustela nigripes*) released onto prairie dog (*Cynomys* spp.) colonies in Montana (MT), South Dakota (SD), and Utah (UT) during 1994–2001 (mean ± SE).

in Arizona, in particular, presented a challenge. Wide spacing between stations was necessary to achieve appropriate coverage of the site, but contact was lost with many animals because of the long distances over which they were tracked. The result may have been a reduced probability of finding dead ferrets, and such known mortalities were the basis for the curves generated. In contrast, Burns Basin in South Dakota provided much better radio-tracking conditions that favored finding cases of mortality (stations were on high points). Overall, highest rates of survival for kits have been in South Dakota as exemplified by our mark-recapture data set. Site characteristics have influenced the efficiency of both spotlight searches and radio telemetry, causing us to adopt experimental designs that compare two or more treatments within sites, to replicate the design over multiple years and sites to achieve adequate sample sizes, and to exercise caution in interpreting results from multiple sites. We might have remained more suspicious about the possible ramifications of our design and potential for confounding without the corroborating results produced by the much larger sample sizes of released ferrets in the mark-recapture portion of the study.

Mark-recapture

Differences between survival rates of males and females were not detected previously (Biggins and others, 1998) in a much smaller data set of 262 ferrets (64 of those animals were included in our present data), although there was speculation that the expected trend toward lower male survival in longer-term data was developing and would be validated with larger sample sizes. Failure to detect such a difference in our data would indeed have been troubling given the male bias in the numbers of animals released (325 males:298 females) and the female-biased composition of free-ranging ferret populations (Forrest and others, 1988). For kits only (comparable to the analysis of Biggins and others, 1998), a gender effect

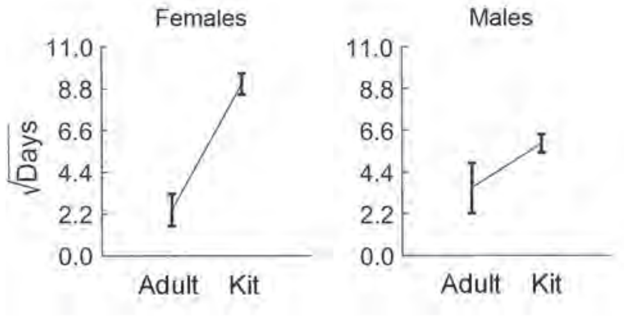

Figure 8. Number of days of known survival for marked adult and young black-footed ferrets (*Mustela nigripes*) calculated using detections from spotlight searches, snow-track searches, and radio telemetry (mean ± SE).

in our data was detectable for both the short-term and long-term evaluations, but the effect became more dramatic over time. Perhaps males became increasingly territorial during the approach of breeding season.

The significant interaction between age and sex classes has potentially nontrivial management ramifications. The interaction may be explained if older age tends to confer greater social status to males than to females, creating a potential problem if adult males have poor long-term survival skills compared to preconditioned male kits. Some older males may be able to competitively exclude younger males, subjecting the latter to temporarily higher mortality. The competition could result in lower overall survival rates for young males without any compensatory increase in long-term survival rates for adult males. If younger males are lost during transitory social interactions with dominant older males, and the older males tend to be lost before breeding season, a shortage of males could result. This phenomenon could occur with concurrent releases of adult and young males, or during releases to augment populations.

General Considerations

Daily survival rates estimated from the 14-day radio-telemetry data set for 94 radio-tagged ferrets seemed reasonably predictive of the 30-day survival rates derived from mark-recapture data on the larger data set of 623 animals. The telemetrically originated survival rates of 42 percent for kits and 11 percent for adults are similar to the overall capture-recapture survival rates of 46 percent for kits and 10 percent for adults. Such comparisons are speculative, however, because of the differing methods and attendant assumptions. First, it is only a reasonable guess to assume that one-third of cases of lost radio contact were due to death of the ferret. Second, the 14-day survival rates were produced under the assumption of a constant hazard rate, an assumption that was repeated to produce the 30-day extrapolation. Hazard rates likely decline postrelease as ferrets with lower fitness are culled and as ferrets learn about their new environment. Over short time spans, the flat hazard rate seems reasonable. Applying a rate generated during the first 2 weeks postrelease to long time spans would be ill-advised. Indeed, our spotlight detections at 150 days (25.9 percent of kits released and 5.7 percent of adults released) were much higher than the respective 3.0 percent and 0.0 percent expectations of the extrapolated daily rates from the first 14 days of radio-tracking data. Third, the mark-recapture estimates are for minimum survival; the actual rate must be somewhat higher assuming we do not count all ferrets present. Finally, the average rates discussed here ignore the implications of statistical modeling, which suggested that rates should be separately estimated for sexes and sites.

Postrelease survival of adult black-footed ferrets might be improved if all young were reared in pens whether they were immediately destined for release or for the captive breeding program. A type of phase-specific learning (Davey, 1989) in which an animal may “imprint” on features of its habitat during a critical period of development has not been investigated for ferrets, but differences in postrelease survival and movements of ferrets as a result of rearing history (Vargas, 1994; Biggins and others, 1998, 1999) arouse suspicion. Even if imprinting is not involved, cultural transmission of important behaviors may be enhanced by a natural environment (Biggins, 2000). Ensuring that each generation has early learning experience in a quasi-natural environment has several potential benefits. Whether or not all kits are raised in pens, increasing the amount of time they spend in outdoor pens could be advantageous. Females that have spent three summers rearing young in the burrows of outdoor pens may make better candidates for release than females without such experience. Perhaps males could be kept in the outdoor pens during much of the remainder of the year, a practice that may accrue additional benefits in reproductive performance (D. Kwiatkowski, oral commun., 1991). Additional investigations of these types of variables might lead to enhanced postrelease survival of captive-reared ferrets.

At this point in the recovery program, black-footed ferret kits seem to have short-term and long-term survival rates at least fourfold higher than those of adult ferrets. On the other hand, ferrets released at age 3 or 4 likely have already exceeded the mean life spans of their wild-born counterparts in established populations. Some female ferrets released as adults have produced litters (in South Dakota and Arizona), and a male released at age 5 in South Dakota survived at least 3.5 years longer, becoming the oldest known ferret in the wild at age 8.5. Such anecdotal information representing extreme cases should carry little weight in decisionmaking, but neither do we presume that data on survival rates for hundreds of ferrets can lead to unequivocal recommendations regarding the advisability of releasing adults. Decisions will need to depend partly on interpreting survival rates of released adults relative to other groups of wild and released ferrets, but philosophical views will continue to exert an influence.

Some conservationists and ethicists may justify extreme means to achieve the goal of preservation and recovery of a species, assuming that the importance of a species is greater than the sum of the rights of its individual constituents (Gunn, 1980). In the words of Rolston (2006, p. 116), "Extinction shuts down the generative processes in a kind of superkilling. It kills forms (species) beyond individuals." Others may set inviolate moral standards regarding the welfare of individuals wherein the "mere size of the relative population of the species to which a given animal belongs makes no moral difference to the grounds for attributing rights to that individual animal or to the basis for determining when that animal's rights may be justifiably overridden or protected" (Regan, 2004, p. 360). Even when thinking is focused on the individual ferret, however, opinions differ. Some emphasize the relative safety of a captive ferret; there is little danger it will miss a meal or, worse yet, become one. This line of ethical reasoning could lead to removing each individual "from its predator-filled natural habitat and providing it with a safe, food-rich environment . . . while exterminating the species" (Agar, 1995, p. 403). The controversy over releasing adult ferrets, however, has a narrower focus and seems to stem mostly from differences of opinion over the relative values of longevity and freedom. Remaining in captivity may allow a zoo animal to avoid an "untimely death" (Regan, 2004, p. 396) but prolongs the "harm" (in the form of "deprivation") that the animal may "suffer as a result of being caged" (Regan, 2004, p. 99). The relative impacts of these "inflictions" and "deprivations" have been contrasted (Regan, 2004, p. 303). Although these philosophical issues may be suitable topics for debate in appropriate forums, extensive discussion of them is beyond the scope of this paper.

Acknowledgments

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References Cited

Agar, N., 1995, Valuing species and valuing individuals: Environmental Ethics, v. 17, p. 397–415.

Anderson, D.R., and Burnham, K.P., 1994, AIC model selection in overdispersed capture-recapture data: Ecology, v. 75, p. 1780–1793.

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Breck, S.W., and Biggins, D.E., 1997, Detecting and eliminating errors in radio-telemetry data sets—a comparison of screened and unscreened data [abs.], *in* Forum on wildlife telemetry: innovations, evaluations, and research needs: Jamestown, N. Dak., Northern Prairie Wildlife Research Center, U.S. Geological Survey, p. 15.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Davey, G., 1989, Ecological learning theory: London, Routledge, 392 p.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Gunn, A.S., 1980, Why should we care about rare species?: Environmental Ethics, v. 3, p. 17–37.

Heisey, D.M., and Fuller, T.K., 1985, Evaluation of survival and cause-specific mortality rates using telemetry data: Journal of Wildlife Management, v. 49, p. 668–674.

Lebreton, J.D., Burnham, K.P., Clobert, J., and Anderson, D.R., 1992, Modeling survival and testing biological hypotheses using marked animals—a unified approach with case studies: Ecological Monographs, v. 62, p. 67–118.

Miller, B., Biggins, D., Wemmer, C., Powell, R., Calvo, L., and Wharton, T., 1990a, Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*). II. Predator avoidance: Journal of Ethology, v. 8, p. 95–104.

Miller, B., Biggins, D., Wemmer, C., Powell, R., Hanebury, L., Horn, D., and Vargas, A., 1990b, Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*). I. Locating prey: Journal of Ethology, v. 8, p. 89–94.

Regan, T., 2004, The case for animal rights: Los Angeles, University of California Press, 425 p.

Rolston, H., III, 2006, Our duties to endangered species, *in* Groom, M.J., Meffe, G.K., and Carroll, C.R., eds., Principles of conservation biology (3d ed.): Sunderland, Mass., Sinauer Associates, p. 116-117.

Vargas, A., 1994, Ontogeny of the endangered black-footed ferret (*Mustela nigripes*) and effects of captive upbringing on predatory behavior and post-release survival: Laramie, University of Wyoming, Ph.D. dissertation, 272 p.

White, G.C., 1983, Numerical estimation of survival rates from band-recovery and biotelemetry data: Journal of Wildlife Management, v. 47, p. 716–728.

White, G.C., and Garrot, R.A., 1990, Analysis of wildlife radio-tracking data: San Diego, Calif., Academic Press, 383 p.

Williams, E.S., Thorne, E.T., Kwiatkowski, D.R., Anderson, S.L., and Lutz, K., 1991, Reproductive biology and management of captive black-footed ferrets (*Mustela nigripes*): Zoo Biology, v. 10, p. 383–398.

Does Predator Management Enhance Survival of Reintroduced Black-footed Ferrets?

By Stewart W. Breck,[1] Dean E. Biggins,[2] Travis M. Livieri,[3] Marc R. Matchett,[4] and Valerie Kopcso[5]

Abstract

Predation on black-footed ferrets (*Mustela nigripes*) is a potential problem at reintroduction sites, causing up to 95 percent of the documented mortality of ferrets. Strategies to reduce mortality due to predation can focus on preconditioning ferrets prior to reintroduction and/or managing predators of ferrets. Biologists have tried three general strategies to control predators at reintroduction sites: (1) selective removal of individual predators, (2) nonselective removal of coyotes (*Canis latrans*), and (3) electric fences to exclude coyotes from release sites. We conducted a post hoc review of data from releases during 1994–2003 at 11 sites in South Dakota and Montana to address whether or not predator management has benefited reintroduced black-footed ferrets. Limited evidence indicates that (1) individual great horned owls (*Bubo virginianus*) can cause significant ferret mortality and that identifying and removing these individuals can be beneficial, (2) lethal control of coyotes may have inverse effects on ferret survival, and (3) electric fencing does not enhance short- or long-term survival of reintroduced ferrets. The data are confounded by a variety of factors, making conclusions tenuous. Well designed studies are needed to properly address the effectiveness of predator management for enhancing ferret survival.

Keywords: black-footed ferret, *Bubo virginianus*, *Canis latrans*, coyote, electric fencing, great horned owl, *Mustela nigripes*, predator control

Introduction

Successful recovery of black-footed ferrets (*Mustela nigripes*) will ultimately depend upon our ability to understand and manage a number of ecological factors (e.g., genetic inbreeding, disease, habitat, and predation) that influence survival, reproduction, and recruitment of ferrets in recovering populations. The role of predators in ecology, conservation biology, and wildlife management has gained increasing recognition as a factor to understand and potentially manage (Estes and others, 2001; Terborgh and others, 1999). For ferrets, mammalian and avian predation has been identified as a critical ecological component in both established populations (Forrest and others, 1988) and reintroduction efforts (Biggins and others, 1998; Biggins, 2000; Biggins, Godbey, Livieri, and others, this volume).

For example, at Meeteetse, Wyo., where the ancestral free-ranging population of ferrets was studied, 57 percent of known mortality of wild ferrets was due to predation (Forrest and others, 1988). Predation by great horned owls (*Bubo virginianus*), golden eagles (*Aquila chryseatos*), and coyotes (*Canis latrans*) was recorded, leading Forrest and others (1988) to conclude that in the Meeteetse ferret population: (1) annual mortality was high, (2) few if any ferrets lived to 3+ years, (3) 59 percent to 77 percent of all juveniles disappeared each year (when disease was not present), (4) adults disappeared at a rate about 80 percent of that seen in juveniles, and (5) predation was the most significant cause of ferret mortality (when disease was not present). For reintroduced animals, predation is equally if not more important, accounting for over 95 percent of the ferrets lost from reintroductions (Biggins, 2000; Biggins, Godbey, Livieri, and others, this volume). For those ferrets killed by predators, coyotes accounted for over 60 percent of the mortality and may have accounted for another 20–30 percent of unconfirmed predation. Badgers (*Taxidea taxus*), great horned owls, and other raptors accounted for a small portion of the predation.

A number of factors likely contribute to the dynamics of predator-ferret interactions, including predator density and behavior, availability of alternative prey, habitat conditions, and, for reintroduced animals, the level of preconditioning individuals receive before being released to the wild. Preconditioning enhanced survival of reintroduced ferrets and Sibe-

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rian polecats (*Mustela eversmannii*; Biggins and others, 1991, 1998, 1999). The foregoing research helped lead to establishment of a general preconditioning program for all ferrets released into the wild. Concurrent with the preconditioning research, biologists and managers from different release sites also tried techniques for managing predators to enhance survival of newly released ferrets. Early studies indicated that mortality of surrogate Siberian polecats was higher in areas with more predators (Biggins and others, 1991). Predator management primarily focused on coyotes and included both lethal and nonlethal techniques. Lethal management primarily involved removing coyotes in and around release areas prior to release of ferrets. To a lesser extent badgers and great horned owls were occasionally killed, mostly in attempts to stop individuals that apparently developed a search image for ferrets. In addition to lethal control, many release sites used electrified fencing to exclude terrestrial predators (primarily coyotes and badgers) for short periods (30–60 days postrelease). The results of these management actions have not been synthesized and published outside of internal reports. Our objective here is to explore existing data to determine if lethal coyote control, electric fencing, or selective removal of individual predators enhanced short-term and/or long-term survival of reintroduced black-footed ferrets.

Study Area and Methods

We synthesized data from black-footed ferret reintroduction sites in Montana and South Dakota and only used data on ferrets that had been preconditioned. Although other data were available from releases in Wyoming, Arizona, and Colorado/Utah, differences in prairie dog (*Cynomys*) species, preconditioning of ferrets, detectability of ferrets, and monitoring methodology from these sites precluded their inclusion in this analysis. In Montana a total of 10 releases occurred from 1994 to 2003, and in South Dakota, 10 releases occurred from 1994 to 1999 (table 1). All releases occurred on black-tailed prairie dog (*C. ludovicianus*) colonies, with higher densities of prairie dogs occurring on the South Dakota sites.

For each release, both short-term (30 days postrelease) and long-term (6–8 months postrelease) estimates of survival were determined by spotlighting ferrets (Campbell and others, 1985). Each survival estimate was based on a multiple night effort in which personnel in vehicles and on foot surveyed release areas with spotlights to detect ferrets. Any ferret detected was identified by using an automatic passive integrated transponder (PIT) reader placed at the burrow containing the animal (Biggins, Godbey, Matchett, and others, this volume). Transponders (i.e., PIT tags) were implanted subcutaneously in each individual prior to release. Survival rates were calculated as the percent of ferrets found alive and thus represent minimum survival estimates. Lack of replication in spotlight surveys over short time spans prevented separate estimation of detection rates and survival rates, precluding the use of more sophisticated methods of survival analysis.

We used short- and long-term minimum survival estimates to evaluate whether lethal coyote control and/or electric fencing increased ferret survival. Lethal coyote control was carried out in a variety of ways and intensities across release sites and years. Some release sites were subjected to extensive coyote removal in and around release areas. At other sites smaller numbers of coyotes were removed in conjunction with disease monitoring, and at some sites no coyote removal was performed (table 1). We categorized the level of coyote control as high, medium, or low. High intensity control combined aerial gunning, opportunistic removal onsite, and disease sampling. Medium intensity control combined opportunistic removal onsite and disease sampling in and around the release area. Low intensity effort involved just disease sampling or no lethal control.

Electric fencing (ElectroNet™; Premier1Supplies, Washington, Iowa) was used in attempts to exclude coyotes from some release sites during some years. ElectroNet is 107 cm in height, powered by 12-V deep cycle batteries, and constructed with 10 alternately charged conductors supported with vertical plastic stays every 30 cm. ElectroNet is designed to exclude mammalian species the size of coyotes and badgers while allowing ferrets and other smaller mammals to move through the fence. Experimental trials of ElectroNet excluded coyotes from bait stations for up to 2 weeks (Matchett, 1995), and telemetry data from ferret reintroduction sites indicated that ElectroNet may have enhanced short-term survival of ferrets within fenced enclosures (Matchett, 1999). We tried to extend knowledge of the utility of ElectroNet by testing for differences in both short- and long-term minimum survival between those reintroduction sites that used ElectroNet and those that did not (table 1). The perimeter of fencing used at reintroduction sites varied from 3.5 km to 13 km and was maintained for a minimum of 30 days postrelease.

We hypothesized that ferrets in areas with higher densities of prairie dogs (i.e., South Dakota), higher levels of coyote control, and electric fencing would have higher estimates of both short- and long-term survival. We generated linear models to evaluate this prediction; competing models included interaction terms and combinations of four explanatory variables (see tables 2 and 3 for a complete list of models). We used likelihood-based methods (Buckland and others, 1997; Burnham and Anderson, 1998) to quantify strength of evidence for alternative models explaining patterns of ferret survival. Estimating the “weight,” or probability that a given model is the best approximation to truth among the models considered, is a means for reporting the relative support for alternative models where the weights from the candidate list of models sum to 1. Thus a model with a weight of 1 has complete support and a model with a weight of 0 has no support (Burnham and Anderson, 1998).

We used Proc GENMOD with the logit link option, which assumes a binomial distribution (SAS Institute Inc., 1999) to analyze each model and create output required to

Table 1. Descriptive data on black-footed ferret (*Mustela nigripes*) survival (short-term = 30 days, long-term = 6–8 months) and predator control efforts (high, medium, or low) from 20 release sites in Montana and South Dakota.

Release area and year	Number of ferrets released	Short-term survival	Long-term survival	Number of coyotes removed	Electric fence used?
MT 94	17	0.47	0.41	Medium	No
MT 95	33	0.61	0.33	High	Yes
MT 96	39	0.56	0.15	High	Yes
MT 97	20	0.55	0.20	Medium	Yes
MT 98	21	0.43	0.14	Medium	Yes
MT 99	23	0.35	0.04	Medium	Yes
MT 01 (BLM 40)	20	0.40	0.15	Low	Yes
MT 02 (BLM 40)	25	0.32	0.16	Low	No
MT 03	37	0.76	0.38	Low	No
MT 03 (BLM 40)	20	0.20	missing	Low	No
SD 94	13	0.38	0.23	Medium	No
SD 95	37	0.30	0.08	Medium	No
SD 96 (Agate)	15	0.53	0.07	High	Yes
SD 96 (Burns)	24	0.29	0.13	High	Yes
SD 97 (Kosher)	21	0.76	0.24	Medium	Yes
SD 97 (Sage)	36	0.86	0.69	Medium	Yes
SD 98 (Agate)	25	0.88	0.28	Low	No
SD 98 (Sage)	15	0.73	0.33	Low	No
SD 99 (Hecktable)	36	0.86	0.44	Low	No
SD 99 (Sage)	12	0.75	0.50	Medium	No

calculate Akaike's Information Criterion (AIC) values. We used ferrets as replicates ($n = 489$) and performed a separate analysis for short- and long-term survival data. For each analysis we assessed the goodness-of-fit by calculating the deviance on the global (fully parameterized) model. We used $\hat{c}$ (deviance/df) to adjust for overdispersion (i.e., lack of fit) and used the small-sample correction of AIC ($QAIC_c$; Lebreton and others, 1992; Burnham and Anderson, 1998) to rank the models and generate an estimate of the weight. We based inferences of survival on the top model.

Results

General patterns in the data show that: (1) both short- and long-term minimum survival estimates have increased in latter years of reintroduction efforts (this was especially true in South Dakota; see table 1); and (2) there was a great deal of variation in estimates of survival across sites and years (short-term low = 20 percent, short-term high = 88 percent; long-term low = 4 percent, long-term high = 69 percent).

Deviance for both global models (short- and long-term analyses) was large (35.5 and 32.7, respectively; $P < 0.001$) indicating that overdispersion was problematic (i.e., fit of model was not good). Based on $QAIC_c$ weights (tables 2 and 3), both short- and long-term minimum survival of reintroduced ferrets were supported by models showing a difference primarily between levels of coyote control and fencing. Ferret survival was inversely related to coyote control with releases that had the highest levels of control showing approximately 12 percent lower minimum survival compared to the lowest levels of control for both short- and long-term analyses (figs. 1 and 2). Evidence of the effectiveness of electric fencing was opposite of what we predicted; ferrets released in areas with fencing showed lower short- and long-term minimum survival than ferrets released in areas without fencing, 3 percent and 5 percent, respectively (figs. 1 and 2). The variable site was not a factor in either analysis, indicating no detectable differences in minimum survival between release sites. There was only weak evidence that survival of ferrets differed between States (i.e., the variable State was part of the 2nd ranked model in the long-term analysis; table 3), indicating differences in prairie dog density between States did not appear to influence survival.

Table 2. Results of the Akaike's Information Criterion (AIC) model selection procedure to determine the model that best explains 1-month survival patterns of reintroduced black-footed ferrets (*Mustela nigripes*), 1994–2003. NPAR is the number of parameters, $QAIC_c$ is a version of AIC adjusted for overdispersion, $DELQAIC_c$ is the difference in QAIC relative to the smallest value in the set, and Weight is an estimate of the likelihood of each model (Burnham and Anderson, 1998). Variables in the models are: fence (present or not), coyote (level of lethal coyote control: low, medium, high), State (Montana or South Dakota), and site (eight different release sites). Dot indicates a model that only includes an intercept (i.e., no explanatory variables). The symbol * indicates an interaction between two variables, and | indicates all possible combinations of the variables.

Model	NPAR	$QAIC_c$	$DELQAIC_c$	Weight
Fence coyote	4	123.41	0.00	0.51
Fence	2	124.93	1.52	0.24
Coyote	3	125.55	2.14	0.18
Dot	1	128.85	5.44	0.03
State fence State*fence	4	129.00	5.59	0.03
Fence coyote fence*coyote	5	132.18	8.77	0.01
State fence	3	133.20	9.79	0.00
State coyote	4	136.25	12.84	0.00
State	2	137.76	14.34	0.00
State fence coyote	5	139.17	15.76	0.00
State coyote State*coyote	6	166.83	43.42	0.00
State|fence State|coyote fence|coyote	9	222.85	99.44	0.00
Site	8	346.79	223.38	0.00

Table 3. Results of the Akaike's Information Criterion (AIC) model selection procedure to determine the model that best explains long-term (6–8 months) survival patterns of reintroduced black-footed ferrets (*Mustela nigripes*), 1994–2003. NPAR is the number of parameters, $QAIC_c$ is a version of AIC adjusted for overdispersion, $DELQAIC_c$ is the difference in QAIC relative to the smallest value in the set, and Weight is an estimate of the likelihood of each model (Burnham and Anderson, 1998). Variables in the models are: fence (present or not), coyote (level of lethal coyote control: low, medium, high), State (Montana or South Dakota), and site (eight different release sites). Dot indicates a model with only an intercept (i.e., no explanatory variables). The symbol * indicates an interaction between two variables, and | indicates all possible combinations of the variables.

Model	NPAR	$QAIC_c$	$DELQAIC_c$	Weight
Fence coyote	4	130.67	0.00	0.484
State fence coyote	5	132.98	2.30	0.153
Fence coyote fence*coyote	5	133.16	2.48	0.140
Fence	2	134.31	3.64	0.078
Coyote	3	135.39	4.72	0.046
State fence	3	135.47	4.80	0.044
Dot	1	136.68	6.00	0.024
State coyote	4	138.84	6.17	0.022
State	2	139.60	8.93	0.006
State fence State*fence	4	140.79	10.12	0.003
State coyote State*coyote	6	143.15	12.47	0.001
State|fence State|coyote fence|coyote	9	193.08	62.41	0.000
Site	8	227.04	96.37	0.000

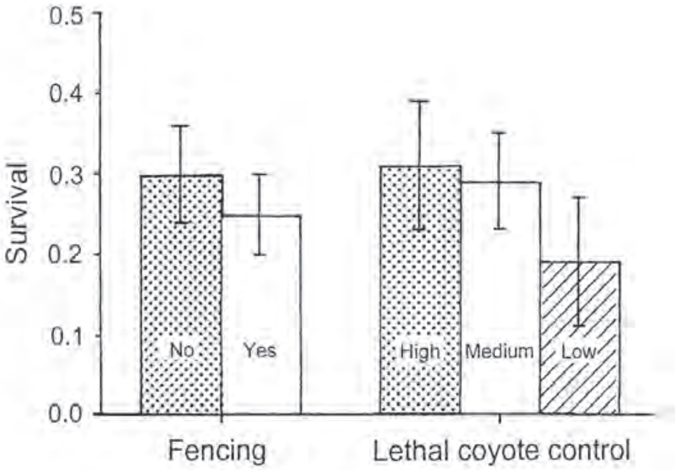

Figure 1. Estimates of short-term (1 month) minimum survival of reintroduced black-footed ferrets (*Mustela nigripes*) for two explanatory variables: fencing (present or not) and lethal coyote control (low, medium, and high). In total, 489 ferrets were released from different sites in Montana and South Dakota from 1994 to 2003. Error bars represent 95% confidence intervals.

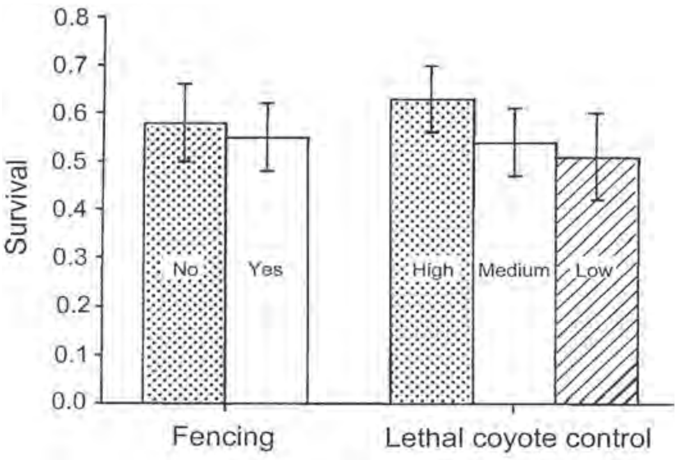

Figure 2. Estimates of long-term (6–8 months) minimum survival of reintroduced black-footed ferrets (*Mustela nigripes*) for two explanatory variables: fencing (present or not) and lethal coyote control (low, medium, and high). In total, 489 ferrets were released from different sites in Montana and South Dakota from 1994 to 2003. Error bars represent 95% confidence intervals.

Discussion

A general pattern that emerged from the data was that estimates of both short- and long-term survival were highly variable even in later years of releases. Variation in survival could be due to a number of factors, including differences in habitat quality, random variation, measurement error, and differences in predation pressure. One factor relating to predators that may have contributed to variation in survival estimates is the role of one or a few problem individuals. Here we define problem individuals as predators that seem to develop a search image for ferrets, consequently becoming disproportionately more successful than other predators at finding and killing ferrets. Critical to the discussion of problem individuals is the realization that mortality of single animals has a larger effect in small populations than in larger populations (Krebs and others, 1995; Krebs, 1996). Thus, it is possible for one or a few individual predators to have a large overall effect on a small population of reintroduced ferrets. A likely example of problem individuals was seen in South Dakota during the 1996 releases (table 1). Nearly half (11 of 24) of the known mortalities that occurred during that release season were caused by one to three great horned owls. In response to the identified problem, three great horned owls were killed on and around the release site, and no further known mortalities were caused by owls. Problem individuals could explain the pattern observed in Montana in 2003 where one release site had a high short-term survival rate of 76 percent while the other had short-term survival of 20 percent, even though no predation by owls was observed.

Our analyses indicated that the relationship between the level of lethal coyote control and ferret survival was opposite of what we hypothesized; that is, more intensive efforts to remove coyotes related to poorer survival for ferrets. This relationship was apparent for both short- and long-term data (figs. 1 and 2). However, several factors are important to consider before drawing any conclusions regarding these patterns. First, most of the high-level efforts for controlling coyotes occurred in earlier years of releases. Thus, the general increase in estimates of survival over time could reflect improvements in preconditioning of ferrets rather than changes in coyote control. Although no data exist to quantify the “quality” of ferrets released over time, it seems possible that preconditioning programs could have improved as the programs were optimized. Second, our method for categorizing levels of coyote control was not ideal. If future research addresses this question, then quantifying density of coyotes pre- and postremoval would be paramount for relating coyote control to ferret survival. Third, increasing survival over successive years may be an artifact of increasing observer efficiency at detecting ferrets or other factors related to estimating survival. The fundamental problem that gives rise to interpretative difficulties mentioned in factors 1–3 previously (and others) is the unbalanced design. All treatments were not replicated at all sites and certainly not in all years at all sites. For example, the BLM 40 complex had only “low” predator control for all 3 years that ferrets were released. Site-specific impacts of unmeasured factors (e.g., disease) may be misinterpreted as treatment effects. Finally, some of the confusion regarding the effectiveness of predator management stems from poor understanding of coyote ecology and behavior in and around release sites. Almost no reliable information exists on activity patterns, use of prairie dog habitat by coyotes, and response of coyotes to control efforts as it relates to black-footed ferrets.

Nevertheless, it is interesting to speculate on how higher levels of coyote control could cause a decrease in ferret survival. Assuming that killing coyotes creates voids filled by coyotes from surrounding territories, one possibility is that as new individuals begin to establish territories, their movements and behavior enhance the probability of encountering ferrets. Many of the ferrets that have been found killed by coyotes were not eaten, indicating that the interaction between coyotes and ferrets may more accurately be described as a form of competition (i.e., intraguild predation; Holt and Polis, 1997; Palomares and Caro, 1999). In competitive interactions, individual animals may not develop specific search images for competitors but rather respond to competitors in an opportunistic fashion. Creating situations in which coyotes are more active (i.e., filling voids) may enhance encounter rates and create greater threat for ferrets.

Of the tools used to control coyote predation, electric fencing offered the most potential to completely eliminate coyote predation on ferrets. The general impression from biologists working at release sites was that fencing did exclude coyotes. At minimum we expected to see higher short-term survival rates for ferrets at sites that used fencing. We found no evidence, however, that fencing enhanced ferret survival for the short- or long-term; in fact, we detected slightly lower survival rates (figs. 1 and 2) at sites that used fencing. Again we caution against strong interpretation of these data for reasons already mentioned, but a couple of factors may explain this pattern.

First, fencing was only used during earlier years of reintroductions (table 1). Though we tried to control for preconditioning in this analysis, it is possible that ferrets released in later years had better preconditioning that enhanced their survival. Second, we know great horned owl predation had a large effect on survival of ferrets at two sites (Agate and Burns) in South Dakota in 1996, both sites that used fencing. Fencing does not deter avian predation, and in this analysis we were unable to control for owl or other avian predation. If we could have controlled for avian predation, it is possible that we would have detected higher survival of ferrets released in areas with fencing, at least for the short-term. Finally, in years when fencing was used, anecdotal observations indicate that many of the ferrets killed by coyotes occurred when ferrets moved outside the fence boundary. Again we were unable to control for this confounding factor in this analysis.

Our results highlight the need to perform well designed experiments to better elucidate the possible benefit of predator management to enhance black-footed ferret survival at reintroduction sites. The fact that survival of reintroduced ferrets remains highly variable indicates that factors other than preconditioning are important. Based on our understanding of ferret ecology, it is likely that predation is responsible for most of the mortality. Understanding whether or not we can manage this predation pressure remains an important goal for ferret recovery. Equally important to recovery efforts is the need to understand the role that predation plays in established populations of black-footed ferrets. Such data would not only provide direct benefits to ferret conservation by potentially increasing the number of ferrets that could be translocated but would also provide better parameter estimates for modeling exercises that depend upon understanding the role of important ecological forces. The most effective means for determining the role of predation in ferret demography and ecology would be to manipulate predator populations and compare responses to unmanipulated populations. Because coyotes are the most important predator of ferrets, we suggest using electric fencing to exclude coyotes as it offers the most potential to control coyote predation.

For the manager who must decide whether or not to manage predators in and around reintroduction sites, we offer the following recommendations. First, great horned owls view ferrets as prey and probably can develop a search image for ferrets. Problem individuals may have large impacts on a population of reintroduced ferrets. If great horned owls are present in the immediate vicinity of a release area, it may be wise to remove individual owls, and, if possible, remove perch sites as well. Second, there is no evidence that lethal removal of coyotes at the levels of control implemented in previous releases enhances short- or long-term survival of ferrets. Extensive control efforts may eliminate coyotes from release sites, temporarily reducing predation pressure on ferrets. However, rates of recolonization by coyotes after such removal are poorly understood and may have important implications for ferrets. Lethal removal of a few individual coyotes probably will not enhance ferret survival because coyotes are often abundant and possibly because of the way coyotes and ferrets interact. Last, electric fencing appears to be an effective method for excluding coyotes and may offer benefits for reintroduced ferrets as long as the fencing is up and functioning. However, maintaining fencing over the long-term is difficult and expensive; thus, fencing is generally only used for short periods (1–2 months). Once fencing is removed, there is no evidence to suggest that the short-term benefits translate into enhanced long-term survival. Thus, for future reintroductions we do not recommend fencing unless the manager can maintain it for long periods or identify how short-term protection may aid long-term survival of ferrets.

References Cited

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 184 p.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Hanebury, L.R., and Miller, B.J., 1991, Trial release of Siberian polecats (*Mustela eversmanni*): Fort Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 25 p.

Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.

Buckland, S.T., Burnham, K.P., and Augustin, N.H., 1997, Model selection—an integral part of inference: Biometrics, v. 53, p. 603–618.

Burnham, K.P., and Anderson, D.R., 1998, Model selection and inference—a practical information-theoretic approach: New York, Springer-Verlag, 353 p.

Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study black-footed ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.

Estes, J., Crooks, K., and Holt, R., 2001, Ecological role of predators, *in* Levin, S.A., ed., Encyclopedia of biodiversity: San Diego, Calif., Academic Press, p. 857–878.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Holt, R.D., and Polis, G.A., 1997, A theoretical framework for intraguild predation: American Naturalist, v. 149, p. 745–764.

Krebs, C.J., Boonstra, R., and Kenney, A.J., 1995, Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada: Oecologia, v. 103, p. 481–489.

Krebs, C.J., 1996, Population cycles revisited: Journal of Mammalogy, v. 77, p. 8–24.

Lebreton, J.D., Burnham, K.P., Colbert, J., and Anderson, D.R., 1992, Modeling survival and testing biological hypotheses using marked animals—a unified approach with case studies: Ecological Monographs, v. 62, p. 67–118.

Matchett, M.R., 1995, Trials of electronet fencing to exclude coyotes: Lewistown, Mont., U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, 7 p.

Matchett, M.R., 1999, Black-footed ferret recovery activities on the UL Bend and Charles M. Russell National Wildlife Refuges, Phillips County, Montana—1998 annual report and 5-year summary: Lewistown, Mont., U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, 22 p.

Palomares, F., and Caro, T.M., 1999, Interspecific killing among mammalian carnivores: American Naturalist, v. 153, p. 492–508.

SAS Institute Inc., 1999, SAS OnlineDoc®, Version 8: Cary, N.C., SAS Institute Inc.

Terborgh, J.J., Estes, J.A., Paquet, P.C., Ralls, K., Boyd-Heger, D., Miller, D., and Noss, R., 1999, The role of top carnivores in regulating terrestrial ecosystems, *in* Soulé, M.E., and Terborgh, J., eds., Continental conservation—scientific foundations of regional reserve networks: Washington, D.C., Island Press, p. 39–64.


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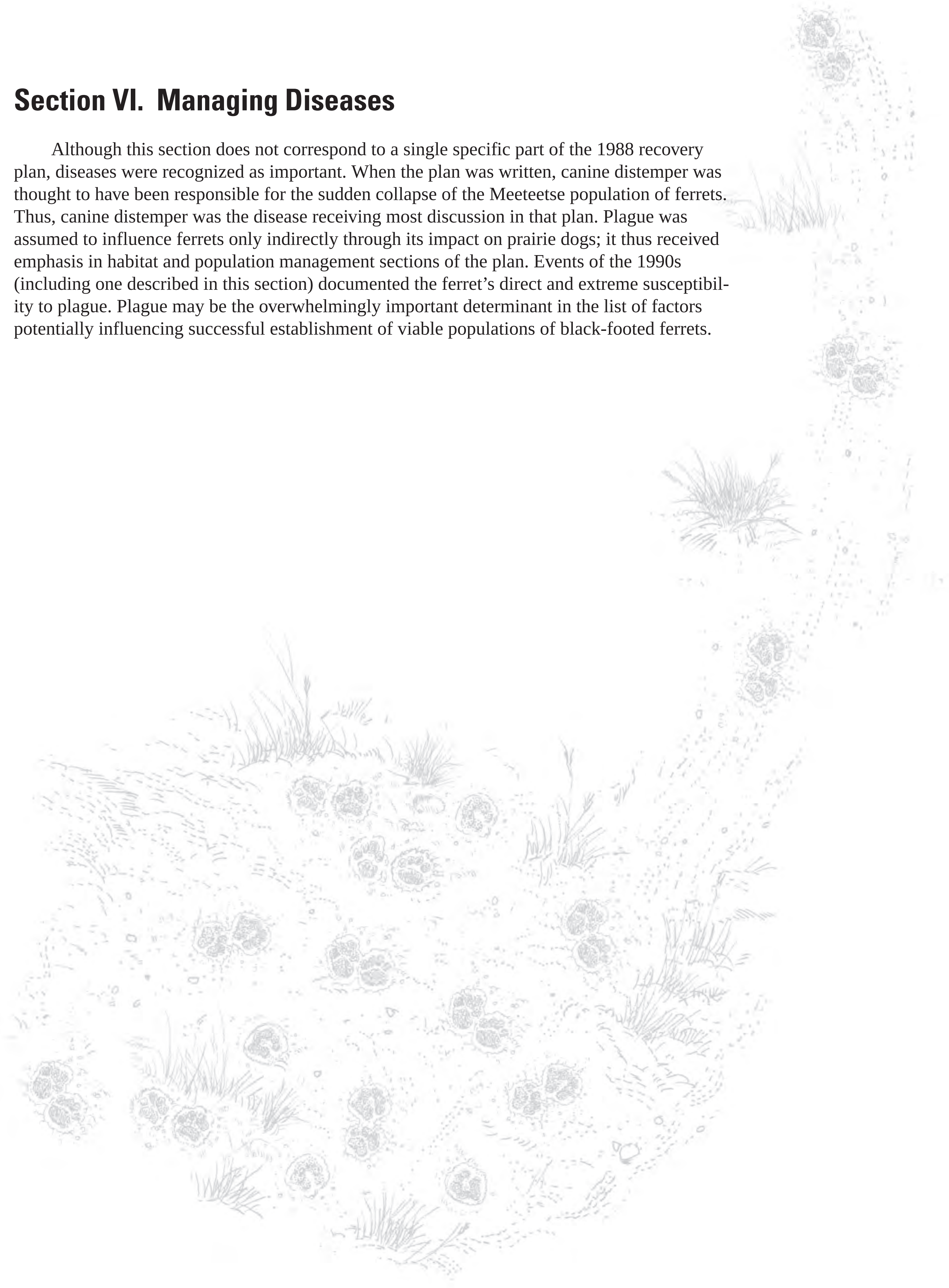
'99

Section VI. Managing Diseases

Although this section does not correspond to a single specific part of the 1988 recovery plan, diseases were recognized as important. When the plan was written, canine distemper was thought to have been responsible for the sudden collapse of the Meeteetse population of ferrets. Thus, canine distemper was the disease receiving most discussion in that plan. Plague was assumed to influence ferrets only indirectly through its impact on prairie dogs; it thus received emphasis in habitat and population management sections of the plan. Events of the 1990s (including one described in this section) documented the ferret’s direct and extreme susceptibility to plague. Plague may be the overwhelmingly important determinant in the list of factors potentially influencing successful establishment of viable populations of black-footed ferrets.



Recent Trends in Plague Ecology

By Kenneth L. Gage[1] and Michael Y. Kosoy[1]

Abstract

Plague (*Yersinia pestis* infection) presents serious risks not only to humans but also to wildlife species such as prairie dogs (*Cynomys* spp.) and the critically endangered black-footed ferret (*Mustela nigripes*). The effects of plague are sufficiently serious to hamper recovery of ferrets and prairie dogs in areas that experience repeated epizootic activity. In order to more effectively manage and reduce plague risks for both wildlife and humans, we must improve our understanding of what factors influence the distribution of plague, the transmission and spread of epizootics, and the ability of the plague bacterium to maintain itself indefinitely in some populations of rodent hosts and their flea (Insecta: Siphonaptera) vectors. This article provides a review of our current knowledge of plague ecology. We also describe how recent research advances are providing significant new knowledge and methodologies that can help us better manage plague risks and reduce the impact of the disease on mammalian populations, including those of conservation interest.

Keywords: disease ecology, flea, plague, rodent, *Yersinia pestis*, zoonosis

Introduction

Plague is a flea-borne zoonotic disease caused by the bacterium *Yersinia pestis* (Gage, 1998). The disease is best known as the cause of devastating pandemics, including the Black Death of the Middle Ages. These same pandemics, as well as other more regional outbreaks, also provide striking demonstrations of plague's ability to spread rapidly across vast geographic areas, a process that occasionally results in the establishment of long-term foci of infection among suitable populations of susceptible mammalian hosts and competent flea vectors. At present, active plague foci are found in many countries in Asia, Africa, and the Americas (Gage, 1998; Tikhomirov, 1999; World Health Organization, 2004). In the United States, evidence of plague infection has been identified during recent decades in mammals or fleas in 17 western States (fig. 1).

Although most evidence suggests that virtually any mammal exposed to *Y. pestis* is likely to become infected, the true vertebrate hosts are certain species of rodents (Pollitzer and Meyer, 1961; Gage and Kosoy, 2005). Plague-related mortality can vary greatly between rodent species and even among populations within the same species. In some rodent species mortality approaches 100 percent (Poland and Barnes, 1979). Although certain other rodents appear to be more resistant to plague, even supposedly resistant populations can experience mortality rates in excess of 40 percent (Rivkus and others, 1973). Mortality can also be high among various nonrodent species found naturally infected with *Y. pestis*. Wild and domestic felines, as well as some lagomorphs (hares, rabbits, and pikas), are extremely susceptible (Gage and others, 1994; Gage and Kosoy, 2005). Identification of high seropositivity rates among other nonrodent species, such as coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and feral hogs (*Sus scrofa*), suggests that these species are at least moderately resistant to plague-related mortality (Gage and others, 1994). While most nonrodent species, with the exception of a few lagomorphs and the house shrew (*Suncus murinus*) of southeastern Asia and Madagascar, are not significant hosts of plague, certain mammalian predators and birds of prey probably play important ecological roles by transporting infected fleas from one region to another (Gage and others, 1994).

Elton's (1958) classic book on the ecology of invasions mentions plague as an example of an agent that can spread explosively across vast areas, infecting not only commensal rats (*Rattus* spp.) and "wild" rodents but also other mammals, including humans (Gage and others, 1995; Gage and Kosoy, 2005). Within the past two decades, an increasing number of biologists have become aware of the devastating effects plague has on certain mammal species of conservation interest (Biggins and Kosoy, 2001a,b). Mortality among infected black-tailed prairie dogs (*Cynomys ludovicianus*) reportedly approaches 100 percent during epizootics, and other prairie dog species (*Cynomys* spp.) also are quite vulnerable to the disease (Kartman and others, 1962; Lechleitner and others, 1962, 1968; Rayor, 1985; Ubico and others, 1988; Anderson and Williams, 1997; Cully, 1997; Cully and others, 1997, 2000; Girard and others, 2004; Stapp and others, 2004). Recent evidence also indicates that plague epizootics can cause significant reductions in genetic diversity among prairie dog populations (Trudeau and others, 2004). In some situations plague has both direct and indirect impacts on wildlife populations. Prairie dogs and their endangered predator, the

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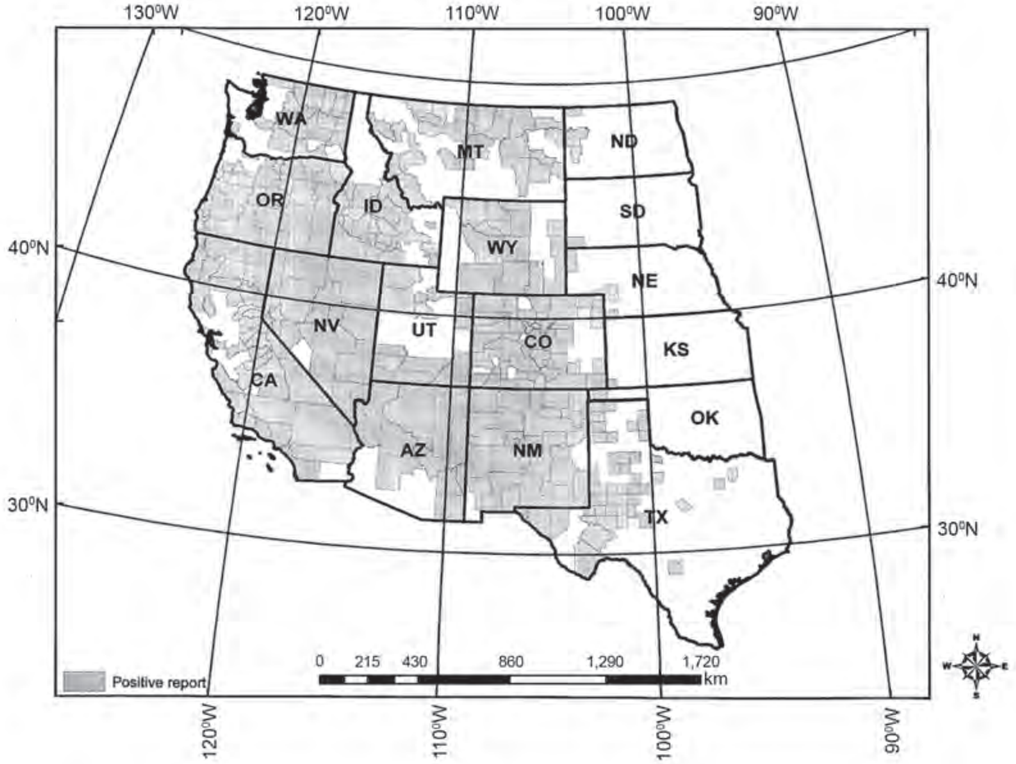


Figure 1. Counties with plague-positive mammals or fleas (1970–present). Figure courtesy of Centers for Disease Control and Prevention.

black-footed ferret (*Mustela nigripes*), are both severely affected by plague, and recovery efforts for black-footed ferrets are hampered not only by the fact that plague outbreaks eliminate the ferrets' prey but also because the ferrets themselves are extremely susceptible to the disease (Williams and others, 1994; Biggins and Kosoy, 2001b; Biggins and Godbey, 2003). The devastating impact of plague on these and other mammalian species of conservation interest has resulted in a renewed emphasis on identifying means for managing plague, including techniques as diverse as insecticidal control of vector fleas and immunization of animals with recombinant vaccines (Creekmore and others, 2002; Seery and others, 2003; Mencher and others, 2004; Rocke and others, 2004). Biggins and Godbey (2003) also discuss partial solutions to the problem of black-footed ferret recovery, including means for increasing breeding in captive populations, increasing survival of released animals, and taking advantage of South Dakota sites that are located slightly east of the known distribution of plague.

In order to more effectively manage and reduce human and wildlife risks associated with plague, we must improve our understanding of the factors that influence transmission, the occurrence and spread of epizootics, and the ability of plague to maintain itself in natural foci. This article provides a brief update on our current knowledge of plague ecology and describes how recent research has contributed to a better understanding of the topic and improved methodologies for studying plague. Also discussed are the many gaps in our knowledge of how plague is maintained in natural foci, what roles certain rodent and vector species play in transmission dynamics, and how environmental factors influence the occurrence, spread, and persistence of epizootics.

The Plague Bacterium and Its Origins

Yersinia pestis is a gram-negative bacterium belonging to the family Enterobacteriaceae. Unlike other members of this group, which are transmitted through fecal-contaminated food and water and live in the guts of their hosts, *Y. pestis* is typically spread from host to host through the bites of infectious fleas and inhabits the blood, as well as lymphatic and reticuloendothelial systems, of its hosts. This dramatic shift in mode of transmission and vertebrate host habitat appears to have been associated, at least in part, with the acquisition of genes that encode virulence and transmission factors. Homologous genes for some *Y. pestis* virulence factors can be found in other species of *Yersinia*, including *Y. pseudotuberculosis*. The origin of genes encoding other virulence or transmission factors is not always clear, but most evidence suggests they were acquired through horizontal transfer of genetic material from other enteric bacteria (Prentice and others, 2001; Gage and Kosoy, 2005). The virulence factors of *Y. pestis* play important roles in enabling host invasion, dispersal within the host, or development of high level bacteremias that greatly increase the likelihood that blood-feeding fleas will imbibe sufficient *Y. pestis* to become infected and later transmit the plague bacterium to other hosts. *Yersinia pestis* transmission factors promote survival of the plague bacterium in the guts of vector fleas and its transmission by these insects. For a more thorough review of virulence and transmission factors and their role in maintaining the natural transmission cycle of plague, see reviews by Perry and Fetherston (1997), Hinnebusch (2003), and Gage and Kosoy (2005).

Until relatively recently, it was believed that the plague bacterium first appeared many millions of years ago, perhaps as early as the upper Oligocene or lower Miocene (Kucheruk, 1965). According to Kucheruk (1965), plague initially arose in cricetid rodents living in semidesert and desert environments. He based these conclusions on an analysis that indicated that the predominant plague hosts in Asia, Africa, and the Americas belonged to the Cricetidae, a family that at the time of Kucheruk's publication included gerbillines, cricetines, arvicolines, and sigmodontines. While this suggestion is still generally accepted, other former Soviet researchers have recently proposed that *Y. pestis* first evolved in marmots (*Marmota* spp.) and their fleas (Suntsov and Suntsova, 2000).

Recent molecular studies clearly indicate that *Y. pestis* is very closely related to the gut microbe *Y. pseudotuberculosis* (Bercovier and others, 1980; Trebesius and others, 1998). The high degree of relatedness between these two bacteria strongly suggests that they have diverged only recently, as suggested by Achtman and others (1999), who proposed that *Y. pestis* might have arisen as a clone of *Y. pseudotuberculosis* only 1,500–20,000 years ago (Achtman and others, 1999; Wren, 2003). This last finding is particularly interesting because of its implications for the degree of coadaptation or coevolution that might have occurred between *Y. pestis* and its hosts and vectors. The recently reported genomic sequences of three *Y. pestis* strains also reveal many interesting features of this bacterium and support the contention that the *Y. pestis* genome is still in a state of rapid flux and might be undergoing reductive evolution as it loses the ability to express certain genes that remain active in *Y. pseudotuberculosis* but are not required for *Y. pestis* to be maintained in a vector-borne transmission cycle (Wren, 2003). Indeed, it has been suggested that the disruption of genes still expressed in *Y. pseudotuberculosis* might be essential for *Y. pestis* to survive in a vector-vertebrate host life cycle (Wren, 2003).

The actual geographic origin of the plague bacterium was a subject of considerable speculation during much of the 20th century. Based on the analysis of plague hosts cited in the previous paragraph, Kucheruk (1965) felt that *Y. pestis* probably appeared in either North American or Asian cricetids. More recent lines of reasoning, however, suggest that a North American origin is highly unlikely. First, epidemiologic evidence strongly indicates that plague did not exist in the United States prior to the last pandemic when rat-infested ships introduced *Y. pestis* to the San Francisco area around 1900 (Link, 1955; Barnes, 1982). Second, microbiological evidence indicates that North American isolates almost invariably reduce nitrates to nitrites but fail to acidify glycerol, which identifies them as belonging to the orientalis biovar that was involved in the late 19th and early 20th century pandemic mentioned above (Devignat, 1951; Guiyoule and others, 1994). Even more convincing results have been provided by recent molecular investigations, including ribotyping and single nucleotide polymorphism analyses, which indicate that United States strains are genetically similar to other orientalis biovar strains collected from areas in other continents that also experienced rat-associated outbreaks during the last pandemic (Guiyoule and others, 1994; Achtman and others, 2004). In general, most lines of evidence, including levels of strain diversity within particular geographic regions, suggest an Asian origin for *Y. pestis*, although the plague bacterium clearly has existed in Africa for more than a millennium and probably considerably longer.

The availability of appropriate methodologies for detecting and analyzing variations among plague strains will have a significant impact on our ability to understand the evolution of plague and how strain differences influence various aspects of *Y. pestis* biology, including its ecology, virulence, and modes of transmission. Early attempts to analyze variation among plague strains relied primarily on phenotypic characteristics, such as reactivities in various biochemical tests, virulence for different types of laboratory animals, production of selected virulence factors, or apparent host associations (Devignat, 1951; Tumanskii, 1957, 1958; Levi, 1962; Stepanov, 1975; Kozlov, 1979). More recently, investigators have analyzed variation among *Y. pestis* strains by using DNA probes, ribotyping, multiple locus variable number tandem repeat assays (MLVA), and analyses of IS100 elements and single nucleotide polymorphisms (Guiyoule and others, 1994; Gorshkov and others, 2000; Klevytska and others, 2001; Motin and others, 2002; Achtman and others, 2004; Girard and others, 2004). Many of the above studies were intended primarily to demonstrate the feasibility of using a particular system for analyzing variation and, thus, examined mostly strains from established reference collections. By contrast, Girard and others (2004) used MLVA to track the spread of plague during an actual epizootic in prairie dogs in northern Arizona. These authors also used their MLVA results, in conjunction with other field and laboratory data, to construct a mutation-rate model that suggested that plague dynamics in their systems consisted of a rapid expansion phase, which was associated with population growth and dispersal, followed by a persistent phase characterized by lower reproduction and dispersal rates. The identification of additional markers should be favored by the recent publication of the complete genomic sequences of three *Y. pestis* strains (Parkhill and others, 2001; Deng and others, 2002; Song and others, 2004).

The phenotypic and genetic studies cited in the previous paragraph identified differences among strains from different foci and host sources, but they fail to answer the question of whether the observed differences among *Y. pestis* strains simply reflect geographic variation or actually provide evidence that regional variants of *Y. pestis* are indeed adapted to a particular host species. Fortunately, the new molecular methodologies described earlier should provide researchers with valuable tools for answering this question as well as other important ecological and evolutionary questions. Analyses of North American strains should be particularly interesting because, as indicated previously, *Y. pestis* apparently has existed in this continent for only a little over 100 years, and the few orientalis biovar strains that were introduced at that time probably were highly similar, having originated in the same region of southwest China. Because the diversity among these invading strains of *Y. pestis* was very low, researchers have an interesting opportunity to examine how *Y. pestis* changes over time and whether this bacterium is likely to exhibit different characteristics, such as increased or decreased virulence, when it is associated with a particular host or vector species.

Plague Transmission Cycles and Maintenance of Plague in Natural Foci

Figure 2 presents a generalized illustration of the natural transmission cycle of plague. In order for flea-borne transmission of plague bacteria to occur, a flea must take a blood meal from a rodent with a heavy *Y. pestis* bacteremia, become infected with plague bacteria, and later transmit this bacterial infection to another susceptible rodent host. Some researchers assume that rodent-to-flea-to-rodent transmission can occur indefinitely in so-called enzootic cycles that cause few apparent deaths among the purportedly resistant rodent hosts (enzootic or maintenance hosts) of these cycles. According to this same concept of plague maintenance and transmission, the disease occasionally spills over to other much more susceptible hosts (epizootic or amplification hosts) that often die in rapidly spreading epizootics, thereby posing increased plague risks for other mammals, including humans (Poland and Barnes, 1979; Poland and others, 1994). As indicated in fig. 2, *Y. pestis* occasionally is transmitted through consumption of infected prey or, perhaps, as a result of inhaling infectious respiratory droplets from animals with pneumonic plague and cough. The roles of these last two modes of transmission in maintaining natural foci have not been determined but are generally assumed to be less important than flea-borne transmission. A few researchers also have proposed that hosts can acquire plague as a result of digging in soil containing viable *Y. pestis* (Mollaret, 1963). Such infections presumably would be acquired through breaks in the skin or inhalation of *Y. pestis* stirred up by an animal's digging activities.

Rodent Hosts of Plague

Based on early observations in India and elsewhere (Pollitzer, 1954), plague initially was believed to exist in

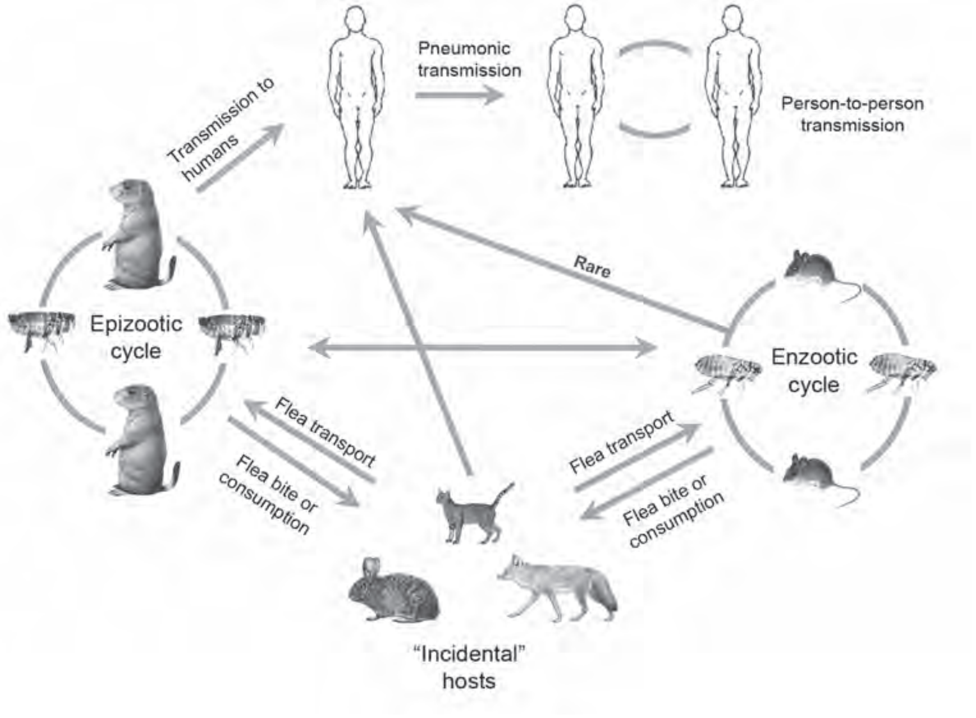


Figure 2. Generalized plague transmission cycle for the United States. Figure courtesy of Centers for Disease Control and Prevention.

nature almost exclusively in commensal rats (primarily *Rattus rattus* and *R. norvegicus*) and rat fleas (primarily *Xenopsylla cheopis*), but it soon became clear that *Y. pestis* also could be found in a variety of wild (noncommensal) rodents and their fleas. In the first decade of the 20th century, McCoy (1908) reported plague among California ground squirrels (*Spermophilus beecheyi*), and others noted soon thereafter that although epizootic activity among rats had largely disappeared, the disease continued to persist in other small mammals around the San Francisco Bay area (Link, 1955). In Asia, Zabolotny (1915) suggested the possibility of wild rodent foci, noting that pneumonic plague outbreaks in Manchuria probably originated from hunters handling tarbagans (*Marmota sibirica*) rather than as a result of human exposure to infectious rat fleas. Later studies confirmed that *Y. pestis* could persist among a variety of rodent species and their fleas without the involvement of commensal rats (Pollitzer, 1954; Pollitzer and Meyer, 1961).

Following the recognition that certain wild rodents are the major hosts of plague, researchers began to ask what characteristics allow particular rodent species to play important roles in the ecology of plague while others play little or no role. At first glance the number of potential rodent hosts is surprisingly high. Pollitzer (1960) identified 203 rodent species or subspecies reported to be naturally infected with *Y. pestis*, a list that could now be slightly extended. However, only a few of these species can be considered truly important hosts of plague, primarily those belonging to the families Sciuridae and Muridae. Among the sciurids, the predominant plague hosts include members of certain genera of burrow-dwelling squirrels (*Spermophilus* [formerly *Citellus*], *Cynomys*, *Ammospermophilus*) and chipmunks (*Tamias*, including *Eutamias* and *Neotamias*). Within the Muridae a number of species in the subfamilies Murinae, Gerbillinae, Arvicolinae, and Sigmodontinae are considered to be important hosts in various regions (Kucheruk, 1965; Gage, 1998; Gratz, 1999).

Among the topics discussed in this paper, probably the most neglected by recent researchers has been the response of native rodent species to *Y. pestis* infection and the roles these animals play in the long-term maintenance of plague foci in different regions. Although many rodents are mentioned in the literature as major plague hosts, the actual evidence to support these claims is often weak, particularly for those putative host species found in certain regions where relatively little research has been done (Gage, 1998; Gratz, 1999). Factors believed to influence the suitability of a particular rodent host for plague include the degree of its population-level resistance to *Y. pestis*-related mortality, its ability to serve as a source of infection for suitable flea vectors, the presence of large numbers of fleas on many members of the host population throughout much of the year, and occupation of burrows or nests that support development and maintenance of high flea populations (Pollitzer and Meyer, 1961; Gage and Kosoy, 2005).

Among these factors, one of the most contentious has been the degree to which population-level resistance to *Y. pestis*-related mortality is essential for the maintenance of plague by one or more rodent species in a particular focus (Pollitzer and Meyer, 1961; Gage and Kosoy, 2005). Host resistance to plague is undoubtedly influenced by many factors, including species, genetic factors within and among populations of a particular species, age, breeding status, prior immunity, physiologic condition, and probably other considerations. When assessing the importance of resistance, it is clear that its presence could favor the survival of host populations in plague-affected areas, although other factors also could operate to reduce mortality and prevent total die-offs among these animals, including the presence of patchy environments that could provide refuges for subpopulations within a larger metapopulation. Seasonal changes in the activities of susceptible hosts or competent flea vectors also might temporarily interrupt or slow down transmission to the point where host populations could be sustained from year to year by recruitment of new individuals (Pollitzer and Meyer, 1961).

One problem encountered in discussing resistance among plague hosts is the somewhat confusing use of the term itself. Host populations that are considered resistant rarely, if ever, are uniformly resistant to *Y. pestis*-related mortality but typically consist of a mixture of somewhat resistant individuals that become infected but recover and other animals that are more susceptible and succumb to plague. For example, mortality rates among great gerbils (*Rhombomys opimus*), which are considered resistant hosts, typically are 40–60 percent (Petrunina, 1951; Rivkus and others, 1973). Although this figure appears high, it is significantly lower than the mortality rates experienced by many other rodents, including other sympatric species of gerbils in the genus *Meriones*. Others have demonstrated that resistance can be associated with past exposure to plague (Birukova, 1960; Thomas and others, 1988; Levi, 1994). Several experiments demonstrated differences in plague resistance between populations of midday gerbils (*Meriones meridianus*) from different sides of the Volga River (Birukova, 1960; Levi, 1994). Levi (1994) compared median lethal doses (LD50) of *Y. pestis* for live-caught gerbils from a population on the west side of the river and another from the east side and found that in three trials, the LD50 values for populations on the west side were 2, 4, and 216 colony forming units (CFUs) while those on the east side of the Volga exhibited LD50 values of 3.397×10^6, 1.000×10^6, and 39.400×10^6 CFUs. Captive-born hybrids of representative individuals (F1 generation) from both populations exhibited intermediate levels of resistance, as did the offspring of these individuals (F2 generation), suggesting that the observed resistance had a genetic basis. According to Levi (1994), these experiments helped explain how midday gerbils are able to serve as primary hosts for plague on the east side of the Volga but have a lesser role west of the river. Interestingly, these same populations of midday gerbils did not differ in their sensitivities to infection with the agents of tularemia and brucellosis. These authors also noted that two populations of another gerbil species, the tamarisk gerbil (*Meriones tamariscinus)*, from the western and eastern sides of the Volga were found to be highly sensitive to plague infection (LD50 values of 6.800 x 10^2 and 5.000 x 10^2 CFUs, respectively).

In North America, Thomas and others (1988) demonstrated that captive-born northern grasshopper mice (*Onychomys leucogaster*) from a plague-free region of Oklahoma were much less resistant to plague than were mice of the same species from a north-central Colorado population that had been exposed to plague. In another North American paper, Quan and Kartman (1956) demonstrated that different populations of deer mice (*Peromyscus maniculatus*) and California voles (*Microtus californicus*) varied in their susceptibility to *Y. pestis*. Differences in susceptibility have been demonstrated to have a genetic basis in California voles (Hubbert and Goldenberg, 1970). Although the above data indicate that populations of some rodent species are highly resistant to *Y. pestis*, others, such as those of the black-tailed prairie dog, nearly always succumb to infection whenever they are struck by plague epizootics (Poland and Barnes, 1979; Biggins and Kosoy, 2001a,b).

Regardless of whether resistant hosts must be present in order for plague foci to persist, flea-borne transmission of plague bacteria among rodents depends on the presence of animals that are capable of serving as sources of infection for feeding fleas. Experimental results indicate that fleas are likely to become infected with *Y. pestis* only after feeding on animals that have very high bacteremias (>10^6 *Y. pestis*/mL blood) (Burroughs, 1947; Engelthaler and others, 2000). In general, animals that have such high bacteremias often appear moribund, and few, if any, survive their infections. Thus, resistant animals that develop little or no bacteremia following infection probably are unlikely to serve as significant hosts for infecting fleas. Resistant individuals that survive infection could, however, still play important ecological roles by serving as hosts for maintaining flea populations and contributing offspring to the next generation of hosts. While many of the offspring of these animals also might be resistant, it is possible that at least some of their littermates will be susceptible.

Some animals might not be completely resistant, at least in the sense of being able to rapidly clear themselves of infection, but rather survive their initial bout of illness and go on to develop a chronic infection with *Y. pestis*. While evidence for chronic infections among North American species is almost nonexistent, the phenomenon has been observed in laboratory rats infected with nonencapsulated plague (F1-minus) strains (Williams and others, 1975; Williams and Cavanaugh, 1983). If wild rodents were chronically infected with fully virulent *Y. pestis* and later experienced a recrudescence of infection, perhaps as a result of breeding stress or decreased immune function in older individuals, they could develop a fatal bacteremia of sufficient magnitude to infect feeding fleas.

As noted above, differences of opinion exist about the importance of resistance among host populations. Some researchers have suggested that the role a particular host population plays in plague maintenance can be inferred largely from its level of resistance (Pollitzer, 1954; Pollitzer and Meyer, 1961; Rall, 1965). For example, great gerbils are believed to be the major hosts of plague in certain central Asian desert foci. The percentage of resistant animals among great gerbil populations in these foci has been reported to be 40–60 percent, a level that is higher than that found in gerbils of the genus *Meriones*, which occur in the same foci (Rivkus and others, 1973). In other situations resistance does not appear to differ greatly among various potential host species, making it difficult to assert that one host is more important than another based strictly on the observed levels of host resistance. For example, resistance was similar among great gerbils (50–80 percent), little susliks (*Spermophilus pygmaeus*) (50–70 percent), and midday gerbils (44–60 percent) in a Kazakh steppe focus (Atshabar, 1999).

Others have argued that the importance of resistance can be overemphasized and that other mechanisms can lead to the persistence of plague among highly susceptible host species (Pollitzer, 1954). While plague might kill most animals in a highly susceptible population, survival can be influenced by age, season, or physical condition, thus allowing some hosts to survive and reproduce. Rodents also might be able to become infected shortly before entering hibernation, develop a latent infection as their body temperatures drop, and then not experience severe illness or die of plague until they reawaken in the spring (Gayskii, 1944; Pollitzer, 1954; Pollitzer and Meyer, 1961). Maevskii and others (1999) also reported that *Y. pestis* could be isolated from the “mummified” carcasses of long-tailed susliks (*S. undulatus*) for 7.5 months after these animals first entered hibernation. Spatial isolation among colonies or subpopulations of highly susceptible hosts also could allow plague to be maintained in metapopulations of these animals (Pollitzer and Meyer, 1961; Gage and Kosoy, 2005). In those foci where highly susceptible hosts live in a mosaic of distinct habitat patches, plague is unlikely to kill all of the susceptible animals in each patch or go from patch to patch without at least some delay, thereby allowing the disease to persist by spreading from patch to patch at a rate that is low enough to allow host populations in previously affected patches to recover before once again being exposed to *Y. pestis* infection.

Types of Plague Hosts

Another unresolved question about the role of different rodent hosts in the natural cycle of plague is whether a single host or multiple hosts are required for long-term maintenance of natural transmission cycles. Fenyuk (1940, 1948) believed that certain rodent species and their fleas could maintain plague in the absence of other rodent species and referred to such animals as primary hosts. Secondary hosts were those species that routinely become infected but are incapable of supporting long-term maintenance of *Y. pestis* in a particular focus. Although secondary hosts are by definition incapable of maintaining plague foci in the absence of primary hosts, some proponents of this concept believe they are important in spreading the disease during epizootics.

Expanding on the primary host hypothesis, Rall (1965) proposed the concept of monohostality wherein maintenance of plague in a particular focus depends on the presence of a single rodent species and its fleas. Probably the most commonly cited examples of monohostal foci are those involving great gerbils in central Asia (Petrov, 1959). Acceptance of this proposal has not been universal, and maintenance of plague in other Asian foci has been suggested by other investigators to involve multiple host species (polyhostal foci) (Kalabukhov, 1965). The "Daurian enzootic area" of central Asia represents a proposed polyhostal focus, with Siberian marmots (*M. sibirica*), Daurian susliks (*S. dauricus*), pikas (*Ochotona* spp.), and voles (*Microtus* spp.) all presumedly playing important roles in maintaining this plague focus (Kalabukhov, 1965). The question of whether various United States foci are monohostal or polyhostal has received little attention. Although existing evidence does not allow firm conclusions to be made, *Y. pestis* infections are frequently identified in multiple rodent species in the western United States, particularly in certain southwestern States (New Mexico, Colorado, Arizona) and some mountainous regions of California and nearby areas (Barnes, 1982; Gage and others, 1995), suggesting that at least some of these foci are polyhostal.

American workers have rarely used the terms primary and secondary hosts or monohostality and polyhostality. Instead, the most commonly cited concept categorizes rodent hosts as either enzootic or epizootic (Poland and Barnes, 1979; Poland and others, 1994). Supporters of this concept suggest that enzootic hosts and their fleas maintain plague during interepizootic periods and share certain features, including heterogeneous population responses to *Y. pestis* infection, low mortality following infection, long multiestrous breeding seasons with high reproductive potential, short life expectancies, flea infestations during all seasons, and a relatively high likelihood that antibody will be detected within the population. The most commonly proposed enzootic hosts are various species of *Peromyscus* and *Microtus*. By contrast, epizootic hosts are considered to have low to moderate resistance to *Y. pestis* infection, often experience high morbidity and mortality when infected, exhibit relatively little population-level heterogeneity to infection, and often experience heavy infestations with one or more species of vector flea that are likely to peak in abundance during the warmer months of the year, which is the time when transmission rates also appear to be highest. Proposed epizootic hosts include various species of *Cynomys*, *Spermophilus*, *Ammospermophilus*, *Tamias*, and *Neotoma* (Barnes, 1982; Gage and others, 1995).

In reality, evidence to support the enzootic-epizootic host concept is often lacking or questionable. Obviously, epizootics with dramatic die-offs do occur among proposed epizootic hosts, but corresponding data to indicate that supposed enzootic hosts, such as deer mice or voles, are essential for the maintenance of plague during interepizootic periods is largely lacking. Another plausible alternative is that plague does not rely on any one host for its maintenance in a particular focus during the intervals between epizootics, but rather circulates at much reduced rates among most, if not all, of the same hosts that commonly become infected during epizootics. Under such circumstances, a fair amount of mortality could occur among these hosts during interepizootic periods but go virtually undetected because of the lack of routine rodent surveillance in most plague-enzootic areas.

The Role of Fleas in Transmitting *Yersinia pestis*

Because of its obvious role in rat-associated bubonic plague outbreaks during the last pandemic, many early studies concentrated on the role of the Oriental rat flea (*Xenopsylla cheopis*) as a vector of plague. Within two decades after Yersin's 1894 discovery of the plague bacterium, Bacot and Martin (1914) demonstrated that *Y. pestis* proliferates in the midgut and proventriculus of an infected flea, forming recognizable colonies within a few days after the fleas ingest an infectious blood meal. They also showed that *Y. pestis* colonies can proliferate in an infected flea to such an extent that its proventriculus, a globular spine-filled structure at the end of the foregut, becomes blocked by a mass of bacteria and blood cell remnants. Once blockage of the proventriculus occurs, blood is no longer able to pass through the foregut to the midgut or "stomach" of the flea, resulting in its eventual starvation. Because the blocked rat flea is starving, it will repeatedly attempt to feed on almost any available mammalian host, including humans. As the flea repeatedly fails in its efforts to ingest blood, it attempts to clear the proventricular blockage by regurgitating, a process that does not clear the block but can dislodge plague bacteria from it. These dislodged bacteria and a small amount of ingested blood are then flushed back into the bite wound, resulting in infection of the host. Fleas that fail to become blocked were found to transmit at much lower rates or not at all, which led to the currently accepted dogma that the only efficient plague vectors are those that become blocked.

Within the past decade the molecular basis by which *Y. pestis* promotes blocking in infected *X. cheopis* has become clear (Hinnebusch, 1997, 2005). Hinnebusch and others (1996) demonstrated that *Y. pestis* strains containing mutations in certain genes (hmsR and hmsH) found in the hemin storage (hms) locus were incapable of forming blockages in infected *X. cheopis* fleas. The hemin storage locus derives its name from the ability of strains that possess a functional hms locus to bind hemin to their surfaces. In general, hemin-binding strains appear to be more "sticky" than strains that cannot bind hemin and are, thus, more likely to form clumps of *Y. pestis* in the flea's gut or adhere to the cuticular spines in its proventriculus (Bibikova, 1977; Hinnebusch and others, 1996). Other investigators have demonstrated that blocking depends on temperature, with fleas rarely becoming blocked, or actually clearing themselves of blockages, when maintained at temperatures above 27.5°C (Cavanaugh, 1971; Hinnebusch and others, 1998).

Additional studies have demonstrated that survival of plague bacteria in flea midguts depends on the expression of a gene (ymt) found on the largest of the three *Y. pestis* plasmids (approximately 110 kb) (Hinnebusch and others, 2002). The product of this gene (Ymt), which is a phospholipase D, has been referred to as murine toxin because of its high toxicity for murines (rats and mice) but not other types of rodents or mammals belonging to other orders. The study by Hinnebusch and others (2002), however, suggests that the true function of Ymt is to promote the survival of *Y. pestis* in the flea vector and that its toxicity for murines is merely coincidental. Even more recent studies have suggested that colonization of flea guts by *Y. pestis* might depend on biofilm formation by the plague bacterium (Darby and others, 2002; Jarrett and others, 2004).

This research has greatly improved our understanding of how *Y. pestis* promotes its transmission by flea vectors, but we still have little knowledge of why some flea species, including those found on wild rodents and presumed to be important vectors, vary so greatly in their ability to transmit plague (Gage and Kosoy, 2005). Taxonomic affinities appear to provide little guidance, as demonstrated by the pulicid fleas of the genus *Xenopsylla*. The Oriental rat flea (*X. cheopis*) and a less widely distributed African rat flea (*X. brasiliensis*) are both highly efficient vectors, but their congener *X. astia*, which is common on rats in the Indian subcontinent and southeastern Asia, is a very poor vector (Pollitzer, 1954). Many decades ago, it was hypothesized that the structure or arrangement of the proventricular spines might be important determinants of a flea's ability to transmit *Y. pestis* (Eskey and Haas, 1940). In support of this contention, Korzun and Nikitin (1997) reported that blocking in a ground squirrel flea, *Citellophilus tesquorum*, was positively associated with high levels of fluctuating asymmetry among the proventricular spines of these fleas.

Although the structure of the proventricular spines might very well influence the blocking process, it does not explain why *Y. pestis* appears to be unable to survive and develop in the guts of certain fleas. Among the poorest plague vectors are a number of flea species commonly associated with man and his domestic animals, including the so-called human flea (*Pulex irritans*), the cat flea (*Ctenocephalides felis*), the dog flea (*C. canis*), and sticktight fleas (*Echidnophaga gallinacea*) (Pollitzer, 1954). For example, *P. irritans* often clear themselves of infection within days after ingesting an infectious blood meal and rarely become blocked. Although these insects can transmit plague, they appear to do so only when large numbers of fleas are placed on susceptible hosts within a few hours after being allowed to feed on a *Y. pestis*-infected animal, suggesting that hosts are infected through the introduction of plague bacteria on contaminated flea mouthparts (mechanical transmission) rather than by the feeding of blocked fleas (Pollitzer, 1954; Blanc, 1956). It should be noted that despite its poor vector competency, some authorities believe that *P. irritans* is a significant vector of plague to humans in those situations where people live in unsanitary, heavily flea-infested homes that are often shared with domestic animals (Pollitzer, 1954; Blanc, 1956). These findings raise the possibility that infected but unblocked fleas on wild rodents also might transmit plague bacteria under certain circumstances.

Fleas found on wild rodent hosts also vary considerably in their ability to support *Y. pestis* infections and transmit plague bacteria (Eskey and Haas, 1940; Douglas and Wheeler, 1943; Burroughs, 1944, 1947; Holdenried, 1952; Pollitzer, 1954; Kartman and Prince, 1956; Kartman, 1957; Kartman and others, 1958a,b; Pollitzer, 1960; Pollitzer and Meyer, 1961; Engelthaler and others, 2000). While some wild rodent fleas appear to block at high rates and become infectious soon after ingesting a *Y. pestis*-containing blood meal, other species require considerably longer periods of time to become blocked. The time required for blocking to occur in some species is sufficiently long that most of the infected fleas are likely to die before block formation actually occurs. A recent comparison of the development of *Y. pestis* infections in *X. cheopis* and *Oropsylla montana*, a ground squirrel flea, demonstrated that *Y. pestis* colonies became established very early in the course of infection in both the proventriculus and the midgut of infected *X. cheopis* (Engelthaler and others, 2000). In *O. montana*, however, *Y. pestis* colonies initially appeared only in the midguts of infected fleas, which meant that the midgut infection had to proliferate and spread considerably before colonization of the proventriculus could occur. Because colonization of the proventriculus is delayed, the average time required for blocking to occur in *O. montana* is much longer than in *X. cheopis*. The failure of many *O. montana* to become blocked and the fact that these fleas transmit at much lower rates than *X. cheopis* are particularly interesting because *O. montana* is considered to be the primary vector of plague to humans in the United States. Published results of experimental infection and transmission studies (see citations at the beginning of this paragraph) done with other species of wild rodent fleas suggest that the situation observed for *O. montana* is more typical than that seen with *X. cheopis*. Of particular interest are the limited studies done with ground squirrel, prairie dog, and woodrat (*Neotoma* spp.) fleas, which typically indicate that most of these fleas are relatively poor plague vectors compared to *X. cheopis* (see earlier citations in this paragraph). While many wild rodent fleas reportedly block and transmit at low rates, a few, such as *Hystrichopsylla dippei*, appear to be quite efficient vectors (Kartman and others, 1958b). Although the studies cited earlier in this paragraph make it obvious that *X. cheopis* is an exceptional plague vector, this does not mean that *Y. pestis* is always successful in its attempts to colonize and establish a stable infection in this flea. Engelthaler and others (2000) found that by 6 weeks after ingesting a *Y. pestis*-infected blood meal, 60 percent of all *X. cheopis* had cleared themselves of infection. Despite this fact, however, the infection rates observed in *X. cheopis*

6 weeks after taking an infectious blood meal were still much higher than those observed in *O. montana* (60 percent versus 15 percent, respectively).

Many of these studies raise questions about whether transmission by blocked fleas is actually essential for the rapid spread of *Y. pestis* during epizootics or for the interepizootic maintenance of plague. One possibility is that in some situations partially blocked fleas could transmit at sufficiently high rates to be important vectors. Burroughs (1947) and Engelthaler and others (2000) demonstrated that *O. montana* fleas were capable of transmitting within 4 days after feeding on an infectious host, a much shorter time than that required for blockage in these species, but perhaps too long for strictly mechanical transmission of viable *Y. pestis* on contaminated mouthparts to occur. Burroughs (1947) and others (Voronova, 1989; Degtyareva and others, 1990; Gan and others, 1990; Bazanova and others, 1991) list additional examples of the transmission of *Y. pestis* by partially blocked or apparently block-free fleas.

The role that mechanical transmission might play in natural foci also should be reexamined. As noted previously, early studies of potential plague vectors indicated that some fleas, such as the human flea, rarely became blocked but occasionally transmitted plague when fleas that had fed on an infected host were quickly transferred in large numbers to susceptible hosts, a finding that is typically interpreted as evidence for mechanical transmission (Pollitzer, 1954; Blanc, 1956). Later studies, particularly those of Burroughs (1944, 1947) and Kartman and others (1958a,b) also provided evidence that common North American rodent fleas are capable of transmitting *Y. pestis* by mechanical means. Quan and others (1953) provided interesting evidence that even *X. cheopis* is capable of mechanically transmitting plague bacteria. Based on the results of the studies noted earlier and others, Burroughs (1947) and Kartman and others (1958a,b) suggested that mechanical transmission might be important, particularly during epizootics when host densities are high and the likelihood that fleas will rapidly transfer from dead hosts to susceptible ones is also high. Kartman and others (1958a,b) further suggested that the bulk of transmission during epizootics occurs through mechanical means while transmission of plague during interepizootic periods is accomplished by those rodent fleas that are capable of becoming blocked and transmitting at high efficiencies. In particular, he cited *Malaraeus telchinum*, a flea that is extremely abundant on mice and voles in some regions of the West, as a likely mechanical vector during epizootics and *Hystrichopsylla dippei*, a far less abundant but much more efficient plague vector, as an important vector during interepizootic periods. Unfortunately, others have not pursued this hypothesis, and it would be very interesting to know whether other “pairs” or groups of fleas play similarly complimentary roles during epizootic and interepizootic periods. It also would be worthwhile to determine whether the rapid rates of transmission observed during plague epizootics in prairie dogs or other highly susceptible hosts are due to mechanical transmission or transmission by blocked fleas. The former can take place virtually immediately after a flea has fed on a heavily bacteremic host, but the latter typically requires an extrinsic incubation period of 2 or more weeks before fleas can become blocked and, therefore, capable of efficiently transmitting. Alternatively, hosts might become infected by consuming other animals that have died of plague or through respiratory contact with hosts that have pneumonic plague.

Although laboratory experiments can help determine whether a particular flea species is likely to be an important vector, other factors also need to be considered in determining the actual role a potential vector will play in nature (Gage, 1998; Gage and Kosoy, 2005). Obviously, fleas that feed on hosts that are seldom infected with plague, or live only in plague-free areas, are unlikely to be important. Fleas that are highly host-specific might be very important for transmitting plague among members of a particular host species but would rarely spread the disease to other hosts. The seasonality and abundance of the flea’s hematophagous adult stage also are likely to be important. Many important vectors occur most abundantly on their hosts during those warm months when plague transmission also peaks. Another potentially important factor is the ability of fleas to survive in off-host environments while waiting for an alternative host to appear.

Maintenance of Plague Between Transmission Seasons and Between Epizootics

Figure 2 provides a basic overview of the plague transmission cycle but unfortunately conveys almost no information on the relative roles different components play in maintaining plague between transmission seasons or during interepizootic periods when little or no *Y. pestis*-related illness is apparent among the normal hosts of the disease. At least four different hypotheses can be advanced for long-term maintenance of plague (Gage and Kosoy, 2005): continuous enzootic transmission among rodent hosts and their fleas at more or less steady rates except during irregularly occurring epizootics; chronic infection of rodents with eventual relapses of the disease in these animals and subsequent infection of vector fleas following these relapses; prolonged survival of infected fleas in host nests or burrows; and indefinite survival of *Y. pestis* in soil, soil protozoa, or perhaps even plant tissues. The following sections discuss the above hypotheses of plague maintenance.

Are Rodents Merely Amplifying Hosts or True Reservoirs of Infection?

In order for plague to be maintained through continuous enzootic transmission, the rodent hosts and flea vectors must both be present and active throughout the year. In temperate regions some plague hosts enter hibernation or become much less active during winter months, which could interrupt the *Y. pestis* transmission cycle. For example, marmots (*M. sibirica* and certain other *Marmota* spp.), which are thought to be critically important plague hosts in some Asian foci, hibernate for many months and, thus, are unlikely to become infected after entering hibernation or support ongoing transmission during this period. If their fleas also become inactive during winter months or lack the opportunity to acquire new infections from hibernating hosts, transmission could be interrupted. One possible solution to this dilemma could be the survival of *Y. pestis* in hibernating animals (Gayskii, 1944; Pollitzer, 1954). According to this hypothesis, a *Y. pestis*-infected animal might enter hibernation prior to becoming ill, thus slowing or temporarily halting the progression of *Y. pestis* infection as a result of the effects of low host body temperature on the growth of the pathogen or its virulence. Upon reawakening in the spring, the infection could reactivate, causing the animal to become ill and develop a *Y. pestis* bacteremia of sufficient magnitude to infect feeding fleas, thereby continuing the cycle of rodent-to-flea-to-rodent transmission for another year. While this explanation seems plausible and does have some experimental support, little is known about its importance in natural foci. Also, such an explanation is unlikely to be important in tropical or subtropical foci. If hibernating animals die of plague before reawakening in the spring, it is also possible that plague bacteria could survive in their dried tissues for many months after the animals have died (Maevskii and others, 1999).

According to some investigators, rodents that do not hibernate might develop chronic infections and act as reservoirs for maintaining plague from one transmission season to the next (Pollitzer, 1954; Pollitzer and Meyer, 1961). Experimental evidence suggests that individual great gerbils in central Asia survive infection and then develop granuloma-like lesions in their livers and perhaps other tissues that contain viable *Y. pestis* (Suleimenov, 2004). These plague bacteria-containing lesions can reportedly persist for many months, thereby allowing latent infections to become reactivated during the spring as adult hosts experience increased stress due to breeding or decreased immune system function due to old age. Great gerbils that experience reactivation of their infections are believed to circulate sufficient *Y. pestis* in their bloodstream to infect feeding fleas. One of the practical problems encountered in evaluating the importance of presumed chronic infections in rodents under field conditions is whether lesions observed in the tissues of suspected carrier hosts are really indicative of chronic infection or simply a sign of resolving infections.

Some researchers have argued that plague could be maintained through the winter months by continuous transmission between certain hosts and their fleas. Such a pattern of transmission has been proposed for deer mice (*P. maniculatus*) and their allies (other *Peromyscus* spp.) or various species of voles (*Microtus* spp. and others) (Poland and Barnes, 1979; Poland and others, 1994). Deer mice and other mice of the genus *Peromyscus* remain active in all seasons, are often infested with fleas during the winter months, and reproduce throughout much of the year, which results in the ongoing introduction of susceptible animals into local mouse populations. Whether populations of *Peromyscus* or voles can indeed maintain plague through continuous rodent to flea to rodent transmission is at present uncertain. In a 13-month study (March 1954–April 1955) of 1,458 *Microtus californicus* found dead in a San Mateo County plague focus, *Y. pestis* was identified in the tissues of these animals during 10 of the 13 months. The only months when positive animals were not identified were December 1954 (n = 52), March 1955 (n = 33) and April 1955 (n = 27) (Kartman and others, 1962). Considering the relatively low number of dead animals examined during those 3 months, *Y. pestis* might have indeed been present all year in at least some voles within this focus.

Fleas as Reservoirs of Plague

While no one disputes that fleas are the only significant vectors of plague, they also could act as long-term reservoirs by maintaining *Y. pestis* in off-host environments during the intervals between transmission seasons or during periods of host hibernation (Gage and Kosoy, 2005). Many studies indicate that infected but unblocked, and even blocked, fleas can survive for many months in off-host environments. In one study, infected *Ctenopthalmus breviatus* survived for up to 396 days when held on wet sand at temperatures of 0–15°C (Golov and Ioff, 1926, 1928). Other studies indicated that *Oropsylla silantiewei* could survive for as long as 558 days without feeding while *Citellophilus tesquorum* and *Neopsylla setosa* did so for 275 and 180 days, respectively (cited by Kozlov, 1979). Sharets and others (1958) reported that *Rhadinopsylla ventricosa* fleas remained infected with *Y. pestis* for at least 420 days. Bazanova and Maevskii (1996) succeeded in maintaining more than half of all *C. tesquorum altaicus* fed on infected susliks (*Spermophilus undulatus*) over a period from mid-September to mid-June, which provided sufficient time for these fleas to survive through the hibernation period of their hosts. One female in their experiments survived through two winters, living for a total of 411 days after being fed on an infected suslik. Even more importantly, when infected *C. tesquorum altaicus* that had been starved through the hibernation period of their hosts were later allowed to feed, they succeeded in transferring plague to these animals, thus demonstrating that these fleas could act as both vectors and reservoirs of infection. In North America, Kartman and others (1962) reported the recovery of infected *Oropsylla labis* (syn. *Opisocrostis labis*) and *O. tuberculata cynomuris* (syn. *Opisocrostis tuberculatus cynomuris*) from abandoned prairie dog burrows for more than a year after their hosts had died of plague.

Survival of Plague in Soils, Soil Protozoa, Plant Tissues, or Other Unusual Sites

Some investigators have proposed that plague might survive during interepizootic periods in the soil of burrows (Mollaret, 1963). In one experiment, four species of gerbils (*Meriones libycus*, *M. persicus*, *M. tristrami*, and *M. vinogradovi*) developed plague after being allowed to dig burrows in laboratory enclosures containing soils contaminated on the previous day with *Y. pestis* in a broth culture (Mollaret, 1963). In other experiments, it was claimed that plague survived many months in both sterilized and nonsterilized soils (Mollaret, 1963; Baltazard, 1964). According to supporters of this hypothesis, rodents can become infected by burrowing in soils that are contaminated with the remains or excreta of infected mammals or fleas. Other researchers have expressed skepticism about this hypothesis, noting methodological concerns about the few studies that have been advanced in its support or that the observed patterns of disease spread and host population recovery often fail to agree with the suggestion that new epizootics are initiated through contact of animals with contaminated soils (Gage and Kosoy, 2005). Also, unlike anthrax or certain other soil-dwelling organisms, *Y. pestis* does not form a sporelike structure, and most evidence suggests that plague bacteria die relatively quickly outside their hosts or vectors (Brubaker, 1991; Perry and Fetherston, 1997). Recently, some have presented evidence that plague might be able to survive in soil protozoa rather than in a free state in soils (Nikul'shin and others, 1992; Nersesov and Tsikhistavi, 1997; Domaradsky, 1999; Pushkareva, 2003). Recent studies also have shown that plague bacteria can form biolfilms on a nematode species (*Caenorhabditis elegans*) commonly used in laboratory studies (Darby and others, 2002), but we know of no evidence indicating that soil nematodes become infected under natural conditions. Others have suggested that *Y. pestis* might survive in plant tissues (Rivkus and others, 1993; Litvin, 1997) or in a latent nonculturable state in soils (Suchkov and others, 1997). Although none of these hypotheses has received strong support, they cannot be completely rejected on the basis of currently available data and are worthy of additional research.

Factors Affecting Rates of Plague Transmission and Incidence of Epizootics

One of the most striking aspects of plague is its ability to spread explosively among susceptible animal populations and across landscapes during epizootics. Almost equally striking is the fact that these relatively brief periods of intense transmission are followed by much longer intervals when the lack of obvious mortality among highly susceptible hosts makes it seem as if the disease has completely disappeared from a particular focus. In most instances, however, at least some *Y. pestis* transmission can still be identified in the suspect area through use of a sensitive monitoring technique, such as serosurveys of coyotes or other rodent-consuming carnivores (Gage and others, 1994). While much remains to be learned about the conditions that lead to plague epizootics or halt their progress, transmission rates can be affected by such factors as host resistance, densities of host and vector populations, the length of time that *Y. pestis* can persist in off-host flea populations, the vector competency of local flea species, the length of the extrinsic incubation period before fleas become infective for hosts, the likelihood that rodents will become chronically infected, periods of host inactivity (hibernation or aestivation), and seasonal changes and other climatic factors that influence the timing of host and vector life cycles as well as their survival and reproduction (Pollitzer, 1954; Pollitzer and Meyer, 1961; Poland and Barnes, 1979; Poland and others, 1994; Gage, 1998; Gage and Kosoy, 2005).

One of the most important questions in plague ecology is what conditions lead to the onset of epizootics. Modeling studies of human rat-associated plague suggest that if plague can persist in small rat subpopulations, it will spill over at irregular intervals to other susceptible rat subpopulations, causing epizootics and increased risks of flea-transmitted bubonic plague in humans (Keeling and Gilligan, 2000a,b). In these studies, persistence was favored by a high proportion of resistant individuals, and short-lived epizootics occurred when plague was introduced into subpopulations composed primarily (>80 percent) of susceptible individuals. In a more recent modeling study using rodent plague surveillance data from Kazakhstan, Davis and others (2004) reported that the invasion and persistence of plague in great gerbil populations was related to rodent density. They also found that as populations fell below certain thresholds, plague was likely to disappear from an area that had been invaded earlier in the course of an epizootic.

The suggestion that rodent population densities affect the invasion and persistence of plague in host populations is not surprising but still leaves open the question of what factors initially cause rodent populations in plague foci to increase and epizootic activity to become likely. Human plague risks typically increase greatly during epizootics, and the occurrence of increased numbers of human cases is generally believed to reflect increased epizootic activity. Parmenter and others (1999) analyzed human plague in New Mexico and found that human risks were correlated with increases in cool season precipitation from the previous year. They attributed this increase in human risk to a trophic cascade effect where increased cool season precipitation led to increased food availability for rodents. It was hypothesized that as food availability increases, so do survival and reproduction of rodent hosts and perhaps flea vectors of plague. In agreement with the results of Davis and others (2004), they postulated that increased rodent numbers increase the risk of epizootics, as well as human cases. In a later study, Enscore and others (2002) demonstrated that both late winter precipitation and threshold temperatures were associated with human plague risks in the Four Corners region of the American Southwest. These last authors suggested that the trophic cascade model of Parmenter and others (1999) be modified to include threshold temperature effects that might affect not only rodent populations but also flea survival and reproduction. In particular, they suggested that years with exceptionally high numbers of days above certain threshold temperatures were likely to be those with low flea populations because of the negative effects of hot summer temperatures on flea survival and reproduction, or perhaps the ability of these insects to transmit plague (Cavanaugh, 1971; Cavanaugh and Marshall, 1972; Enscore and others, 2002). Collinge and others (2005b) attempted to test the generality of the trophic cascade model (Parmenter and others, 1999) as modified by Enscore and others (2002) and found that the occurrences of reported plague events in prairie dogs were not associated with certain climatic variables in Boulder County, Colo., but were associated with precipitation and temperature effects in a Phillips County, Mont., site. The authors concluded that the timing and magnitude of precipitation and temperature might influence the occurrence of plague in some but not all areas. They also reported that the best climatic predictors in the Montana site corresponded well with those noted in the above studies of human plague cases in the southwestern United States. In another Colorado study, Stapp and others (2004) demonstrated that epizootics in prairie dogs living on grasslands in north-central Colorado were associated with El Niño events.

Landscape Ecology of Plague

The influence of landscape structure on plague distribution and dynamics has been investigated in only a few of the world's plague foci. Bibikov and others (1963) stated that localities where plague infection can be maintained for a long period of time occupy relatively small portions of the territories that are endemic for plague, and speculated that, for unknown reasons, these sites present more auspicious conditions for the circulation of *Y. pestis* than other sites that are only affected sporadically. In other studies, Alexeev (1991) and Karimova (2002) used landscape characteristics for typing plague foci in desert zones of Kazakhstan and central Asia. Medzykhovsky and others (2001) demonstrated an association between the distribution of plague epizootics in the trans-Uralian steppe regions of eastern Kazakhstan and certain soil and grass characteristics. Serzhanov and others (1982a) found that places where plague persists over long periods of time in central Asian deserts are closely associated with landscapes characterized by abundant underground water lying near the surface (hydrologic lenses). These authors also demonstrated a correlation between the dynamics of plague epizootics and groundwater characteristics in nine different landscapes in Turkmenia. Based on these observations, Serzhanov and others (1982b) proposed the use of hydrothermal indices for the ecological typing of plague foci. In another interesting study, Rotshild (2001) hypothesized that levels of trace metals in natural environments influence the distribution and occurrence of plague. His hypothesis was based on multiple observations in the Altai Mountains, Tuva (eastern Siberia), the Kyzyl Kum desert in Uzbekistan, and a sandy semidesert area of the Caspian lowlands where he found correlations between epizootic plague activity and decreased or increased concentrations of Fe, Co, and Ti and low concentrations of Cu, Ni, and V.

In the United States, plague foci are known to occur in a variety of landscapes in numerous western mountain ranges, the High Plains, and intermountain grasslands (Barnes, 1982). Although plague might make brief epizootic intrusions into some areas, it remains conspicuously absent from certain extremely hot desert regions of the southwestern States, including the Sonoran Desert in southern Arizona. Although the reasons for plague's absence in these areas are unknown, it is tempting to speculate that the extremely hot, dry conditions in these desert areas are likely to limit transmission by fleas because these insects probably face severe desiccation when they are not closely associated with a host or protected burrow system or when they attempt to quest at burrow entrances in such exceptionally hot and dry environments.

A so-called "plague line" appears to exist at about the 100th meridian of longitude, a line that along much of its length marks the zone of transition from the tall grass prairies to the short grass habitats of the High Plains (Barnes, 1982). Among the factors that might influence the location of this "plague line" are rodent and flea diversity and changes in burrow microclimates or other features of burrow ecology. Although some recognized plague hosts occur on the plains, including black-tailed prairie dogs, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), spotted ground squirrels (*S. spilosoma*), and southern plains woodrats (*Neotoma micropus*), the diversity of important plague hosts clearly decreases as one moves away from the Rocky Mountains onto the High Plains. By contrast, numerous rodent hosts of plague occur in relatively close proximity to each other in the lower elevation coniferous woodlands, foothills, and nearby plains. Many of these species, including woodrats, prairie dogs, ground squirrels, and chipmunks, live in burrows or complex nests that are often heavily infested with fleas. Another factor that might be important is the habitat complexity found near the Rockies and on High Plains sites nearest to these mountains. The more varied and patchy habitats around the Rockies could provide partial barriers and slow the movement of plague from one habitat to another, thus providing a limited refuge for some rodent populations and increasing the likelihood that sufficient hosts will survive epizootics and keep transmission going from one season the next. As one moves on to the High Plains, however, the habitats appear to be more homogeneous with fewer barriers to the spread of plague, which could result in rapidly spreading epizootics that kill nearly all susceptible rodents and leave few individuals to support ongoing transmission. Plague probably is unlikely to persist in areas with such relatively homogeneous habitats but could, perhaps, repeatedly invade them when widespread epizootics sweep across the landscape.

Regional or local landscape ecology studies are almost nonexistent in the plague foci of the western United States. A single recent study by Collinge and others (2005a) used logistic regression to analyze two long-term data sets on plague occurrence in prairie dogs. The first of their two study sites was located in Boulder County, Colo., a region subject to rapid human development, and the second was in Phillips County, Mont. Associations were found at both sites between plague occurrence, landscape parameters, and colony characteristics. The best models from both sites predicted positive effects on plague occurrence of proximity to colonies that experienced plague and negative effects of road, stream, and lake cover.

Conclusions

Although some important findings, such as those describing how *Y. pestis* promotes its transmission by flea vectors, have occurred in recent years, many aspects of our understanding of plague ecology have progressed little since the mid-20th century. This is surprising when one considers the exciting new advances in many relevant fields or technologies, including molecular biology, immunology, population genetics, microbiology, geographic information systems, remote sensing, and mathematical modeling. Among the many interesting issues that have yet to be addressed satisfactorily are the degree to which *Y. pestis* exhibits adaptations to major hosts and vectors or vice versa, the relative roles of various factors in determining levels of host resistance, the roles many rodent species play in plague maintenance, the structure of plague foci in North America and elsewhere, the true significance of mechanical transmission or the transmission of plague bacteria by partially blocked fleas, the reasons why different flea species vary so greatly in vector competency, and the roles that climatic variables, landscape features, host and vector densities, or other factors play in influencing the spread of plague or the occurrence of epizootics. Fortunately, many of these questions can now be addressed, as interest in plague and funding for its study have increased as a result of recent concerns about the use of plague as a weapon of bioterrorism and the recognition that *Y. pestis* can adversely impact many wildlife species.

References Cited

Achtman, M., Morelli, G., Zhu, P., Wirth, T., Diehl, I., Kusecek, B., Vogler, A.J., Wagner, D.M., Allender, C.J., Easterday, W.R., Chenal-Francisque, V., Worsham, P., Thomson, N.R., Parkhill, J., Lindler, L.E., Carniel, E., and Keim, P., 2004, Microevolution and history of the plague bacillus, *Yersinia pestis*: Proceedings of the National Academy of Sciences, v. 101, p. 17837–17842.

Achtman, M., Zurth, K., Morelli, G., Torrea, G., Guiyoule, A., and Carniel, E., 1999, *Yersinia pestis*, the cause of plague, is a recently emerged clone of *Yersinia pseudotuberculosis*: Proceedings of the National Academy of Sciences, v. 96, p. 14043–14048.

Alexeev, E.V., 1991, Ecological and geographic characteristics of natural foci of plague: Ekologiya, issue 6, p. 45–51.

Anderson, S.H., and Williams, E.S., 1997, Plague in a complex of white-tailed prairie dogs and associated small mammals in Wyoming: Journal of Wildlife Diseases, v. 33, p. 720–732.

Atshabar, B., 1999, Plague biocenosis as ecological system, *in* Kutirev, V.V., ed., Problemy Osobo-Opasnih Infektsii: Saratov, Slovo Press, v. 79, p. 36–44.

Bacot, A.W., and Martin, C.J., 1914, Observations on the mechanism of the transmission of plague by fleas: Journal of Hygiene (London), v. 13 (Plague suppl. III), p. 423–439.

Baltazard, M., 1964, The conservation of plague in inveterate foci: Journal of Hygiene, Epidemiology, Microbiology, and Immunology, v. 120, p. 409–421.

Barnes, A.M., 1982, Surveillance and control of bubonic plague in the United States: Symposia of the Zoological Society of London, v. 50, p. 237–270.

Bazanova, L.P., and Maevskii, M.P., 1996, The duration of the persistence of plague microbe in the body of flea *Citellophilus tesquorum altaicus*: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 2, p. 45–48.

Bazanova, L.P., Zhovtyi, I.F., Maevskii, M.P., Klimov, V.T., and Popkov, A.F., 1991, The seasonal dynamics of blocking in the flea *Citellophilus tesquorum altaicus* from the Tuva natural plague focus: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 1, p. 24–26.

Bercovier, H., Mollaret, H.H., Alonso, J.M., Brault, J., Fanning, G.R., Steigerwalt, A.G., and Brenner, D.J., 1980, Intra- and interspecies relatedness of *Yersinia pestis* by DNA hybridization and its relationship to *Y. pseudotuberculosis*: Current Microbiology, v. 4, p. 225–229.

Bibikov, D.I., Petrov, V.S., and Khrustselevsky, V.P., 1963, On some ecological and geographical patterns in natural focality of plague: Zoologicheskii Zhurnal (Leningrad), v. 42, p. 1306–1316.

Bibikova, V.A., 1977, Contemporary views on the interrelationships between fleas and the pathogens of human and animal diseases: Annual Review of Entomology, v. 22, p. 23–32.

Biggins, D.E., and Godbey, J.L., 2003, Challenges to reestablishment of free-ranging populations of black-footed ferrets: Comptes Rendus Biologies, v. 326, suppl. 1, p. S104–S111.

Biggins, D.E., and Kosoy, M.Y., 2001a, Influences of introduced plague on North American mammals—implications from ecology of plague in Asia: Journal of Mammalogy, v. 82, p. 906–916.

Biggins, D.E., and Kosoy, M.Y., 2001b, Disruptions of ecosystems in western North America due to invasion by plague: Journal of the Idaho Academy of Science, v. 37, p. 62–65.

Birukova, E.S., 1960, Experimental plague in the tamarisk gerbil *Meriones tamariscinus* and the midday gerbil *M. meridianus* from the eastern Caucasian region, *in* Trudy Protivochumnogo Instituta Kavkaza i Zakavkaz’ya 4: Stavropol’, Russia, Stavropol’skoe knizhnoe izdatel’stvo, p. 84–94.

Blanc, G., 1956, Une opinion non conformiste sur la mode de transmission de la peste: Revue d’Hygiene et de Medicine Sociale, v. 4, p. 535–562.

Brubaker, R.R., 1991, Factors promoting acute and chronic diseases caused by yersiniae: Clinical Microbiology Reviews, v. 4, p. 309–324.

Burroughs, A.L., 1944, The flea *Malaraeus telchinum*, a vector of *P. pestis*: Proceedings of the Society for Experimental Biology and Medicine, v. 55, p. 10–11.

Burroughs, A.L., 1947, Sylvatic plague studies. The vector efficiency of nine species of fleas compared with *Xenopsylla cheopis*: Journal of Hygiene, v. 43, p. 371–396.

Cavanaugh, D.C., 1971, Specific effect of temperature upon transmission of the plague bacillus by the Oriental rat flea, *Xenopsylla cheopis*: American Journal of Tropical Medicine and Hygiene, v. 20, p. 264–273.

Cavanaugh, D.C., and Marshall, J.D., Jr., 1972, The influence of climate on the seasonal prevalence of plague in the Republic of Vietnam: Journal of Wildlife Diseases, v. 8, p. 85–94.

Collinge, S.K., Johnson, W.C., Ray, C., Matchett, R., Grensten, J., Cully, J.F., Jr., Gage, K.L., Kosoy, M.Y., Loye, J.E., and Martin, A.P., 2005a, Landscape structure and plague occurrence in black-tailed prairie dogs: Landscape Ecology, v. 20, p. 941–955.

Collinge, S.K., Johnson, W.C., Ray, C., Matchett, R., Grentsen, J., Cully, J.F., Jr., Gage, K.L., Kosoy, M.Y., Loye, J.E., and Martin, A.P., 2005b, Testing the generality of a trophic-cascade model for plague: EcoHealth, v. 2, p. 1–11.

Creekmore, T.E., Rocke, T.E., and Hurley, J., 2002, A baiting system for delivery of an oral plague vaccine to black-tailed prairie dogs: Journal of Wildlife Diseases, v. 38, p. 32–39.

Cully, J.F., Jr., 1997, Growth and life-history changes in Gunnison’s prairie dogs after a plague epizootic: Journal of Mammalogy, v. 78, p. 146–157.

Cully, J.F., Jr., Barnes, A.M., Quan, T.J., and Maupin, G., 1997, Dynamics of plague in a Gunnison’s prairie dog colony complex from New Mexico: Journal of Wildlife Diseases, v. 33, p. 706–719.

Cully, J.F., Jr., Carter, L.G., and Gage, K.L., 2000, New records of sylvatic plague in Kansas: Journal of Wildlife Diseases, v. 36, p. 389–392.

Darby, C., Hsu, J.W., Ghori, N., and Falkow, S., 2002, Plague bacteria biofilm blocks food intake: Nature, v. 417, p. 243–244.

Davis, S., Begon, M., De Bruyn, L., Ageyev, V.S., Klassovskiy, N.L., Pole, S.B., Viljugrein, H., Stenseth, N.C., and Leirs, H., 2004, Predictive thresholds for plague in Kazakhstan: Science, v. 304, p. 736–738.

Degtyareva, L.V., Labunets, N.F., Osipova, S.P., and Shchedrin, V.I., 1990, The ability of flea species on common vole from mountainous Dagestan to transmit and preserve the causative agent of plague: Parazitologiya, v. 24, p. 106–112.

Deng, W., Burland, V., Plunkett, G., III, Boutin, A., Mayhew, G.F., Liss, P., Perna, N.T., Rose, D.J., Mau, B., Zhou, S., Schwartz, D.C., Fetherston, J.D., Lindler, L.E., Brubaker, R.R., Plano, G.V., Straley, S.C., McDonough, K.A., Nilles, M.L., Matson, J.S., Blattner, F.R., and Perry, R.D., 2002, Genome sequence of *Yersinia pestis* KIM: Journal of Bacteriology, v. 184, p. 4601–4611.

Devignat, R., 1951, Variétés de l’espèce *Pasteurella pestis*—nouvelle hypothèse: Bulletin of the World Health Organization, v. 4, p. 247–263.

Domaradsky, I.V., 1999, Is not plague a “protonosis”?: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 2, p. 10–13.

Douglas, J.R., and Wheeler, C.M., 1943, Sylvatic plague studies. II. The fate of *Pasteurella pestis* in the flea: Journal of Infectious Diseases, v. 72, p. 18–30.

Elton, C.S., 1958, The ecology of invasions by animals and plants: London, Methuen and Co., 181 p.

Engelthaler, D.M., Hinnebusch, B.J., Rittner, C.M., and Gage, K.L., 2000, Quantitative competitive PCR as a method for exploring flea-*Yersinia pestis* dynamics: American Journal of Tropical Medicine and Hygiene, v. 62, p. 552–560.

Enscore, R.E., Biggerstaff, B.J., Brown, T.L., Fulgham, R.F., Reynolds, P.J., Engelthaler, D.M., Levy, C.E., Parmenter, R.R., Montenieri, J.A., Cheek, J.E., Grinnell, R.K., Ettestad, P.J., and Gage, K.L., 2002, Modeling relationships between climate and the frequency of human plague cases in the southwestern United States, 1960–1997: American Journal of Tropical Medicine and Hygiene, v. 66, p. 186–196.

Eskey, C.R., and Haas, V.H., 1940, Plague in the western part of the United States: Public Health Bulletin No. 254, 82 p.

Fenyuk, B.K., 1940, Ecological factors of plague focality: Zoologicheskii Zhurnal (Leningrad), v. 19, p. 349–351.

Fenyuk, B.K., 1948, Ecological factors in natural focality and epizootiology of plague in rodents. A role of secondary hosts of plague, *in* Trudi nauchnoi konferentsii posv'yaschennoi 25 letiu Instituta "Mikrob": Saratov, Russia, p. 37–40.

Gage, K.L., 1998, Plague, *in* Collier, L., Balows, A., Sussman, M., and Hausler, W.J., Jr., eds., Topley and Wilson's microbiology and microbial infections (9th ed.), vol. 3, Bacterial infections: London, Arnold, p. 885–904.

Gage, K.L., and Kosoy, M.Y., 2005, Natural history of plague: perspectives from more than a century of research: Annual Review of Entomology, v. 50, p. 505–528.

Gage, K.L., Ostfeld, R.S., and Olson, J.G., 1995, Nonviral vector-borne zoonoses associated with mammals in the United States: Journal of Mammalogy, v. 76, p. 695–715.

Gage, K.L., Thomas, R.E., and Montenieri, J.A., 1994, The role of predators in the ecology, epidemiology, and surveillance of plague in the United States, *in* Proceedings of the 16th Vertebrate Pest Conference: Davis, University of California, p. 200–206.

Gan, N.V., Voronova, G.A., Yuzvik, L.N., and Belyaeva, V.A., 1990, The capability of *Rhadinopsylla rothschildi* and *R. dahurica* fleas as vectors of plague pathogen in Transbaikal natural focus: Parazitologiya, v. 24, p. 151–154.

Gayskii, N.A., 1944, Infection and immunity in hibernating animals, *in* Izvestiya Irkutskogo Gosudarstvennogo protivochumnogo instituta Sibiri i Dal'nego Vostoka, Irkutsk, v. 5, p. 82–123.

Girard, J.M., Wagner, D.M., Vogler, A.J., Keys, C., Allender, C.J., Drickamer, L.C., and Keim, P., 2004, Differential plague-transmission dynamics determine *Yersinia pestis* population genetic structure on local, regional and global scales: Proceedings of the National Academy of Sciences, v. 101, p. 8408–8413.

Golov, D., and Ioff, I., 1926, Suslik fleas as preservers of plague infection in winter: Reviews Microbiology, Saratov, v. 5, p. 239–251.

Golov, D., and Ioff, I., 1928, On the question of the role of the rodent fleas in the southeastern part of the USSR and the epidemiology of plague, *in* Proceedings of the 1st all-Russian anti-plague conference: Saratov, Mikrob Central Antiplague Institute, p. 102–105.

Gorshkov, O.V., Savostina, E.P., Popov, Y.A., Plotnikov, O.P., Vinogradova, N.A., and Solodovnikov, N.S., 2000, Genotyping *Yersinia pestis* strains from various natural foci: Molekulyarnaya Genetika, Mikrobioliogiya i Virusologiya, issue 3, p. 12–17.

Gratz, N.G., 1999, Rodent reservoirs and flea vectors of natural foci of plague, *in* Plague Manual: Geneva, Switzerland, World Health Organization, p. 63–96.

Guiyoule, A., Grimont, F., Iteman, I., Grimont, P.A.D., Lefevre, M., and Carniel, E., 1994, Plague pandemics investigated by ribotyping of *Yersinia pestis* strains: Journal of Clinical Microbiology, v. 32, p. 634–641.

Hinnebusch, B.J., 1997, Bubonic plague: a molecular genetic case history of the emergence of an infectious disease: Journal of Molecular Medicine, v. 75, p. 645–652.

Hinnebusch, B.J., 2003, Transmission factors: *Yersinia pestis* genes required to infect the flea vector of plague: Advances in Experimental Medicine and Biology, v. 529, p. 55–62.

Hinnebusch, B.J., 2005, The evolution of flea-borne transmission in *Yersinia pestis*: Current Issues in Molecular Biology, v. 7, p. 197–212.

Hinnebusch, B.J., Fischer, E.R., and Schwan, T.G., 1998, Evaluation of the role of the *Yersinia pestis* plasminogen activator and other plasmid-encoded factors in temperature-dependent blockage of the flea: Journal of Infectious Diseases, v. 178, p. 1406–1415.

Hinnebusch, B.J., Perry, R.D., and Schwan, T.G., 1996, Role of the *Yersinia pestis* hemin storage (hms) locus in the transmission of plague by fleas: Science, v. 273, p. 367–370.

Hinnebusch, B.J., Rudolph, A.E., Cherepanov, P., Dixon, J.E., Schwan, T.G., and Forsberg, A., 2002, Role of Yersinia murine toxin in survival of *Yersinia pestis* in the midgut of the flea vector: Science, v. 296, p. 733–735.

Holdenried, R., 1952, Sylvatic plague studies. VII. Plague transmission potentials of the fleas *Diamanus montanus* and *Polygenis gwyni* compared with *Xenopsylla cheopis*: Journal of Infectious Diseases, v. 90, p. 131–140.

Hubbert, W.T., and Goldenberg, M.I., 1970, Natural resistance to plague—genetic basis in the vole (*Microtus californicus*): American Journal of Tropical Medicine and Hygiene, v. 19, p. 1015–1019.

Jarrett, C.O., Deak, E., Isherwood, K.E. Oyston, P.C., Fischer, E.R., Whitney, A.R., Kobayahsi, S.D., DeLeo, F.R., and Hinnebusch, B.J., 2004, Transmission of *Yersinia pestis* from an infectious biofilm in the flea vector: Journal of Infectious Diseases, v. 190, p. 783–792.

Kalabukhov, N.L., 1965, The structure and dynamics of natural foci of plague: Journal of Hygiene, Epidemiology, and Microbiology, v. 9, p. 147–159.

Karimova, T.Y., 2002, Spatial differentiation of natural foci of plague in Sahara-Gobian desert: Uspehi Sovremennoi Biologii, v. 122, p. 422–432.

Kartman, L., 1957, The concept of vector efficiency in experimental studies of plague: Experimental Parasitology, v. 6, p. 599–609.

Kartman, L., and Prince, F.M., 1956, Studies on *Pasteurella pestis* in fleas. V. The experimental plague-vector efficiency of wild rodent fleas compared with *Xenopsylla cheopis*, together with observations on the influence of temperature: American Journal of Tropical Medicine and Hygiene, v. 5, p. 1058–1070.

Kartman, L., Prince, F.M., and Quan, S.F., 1958a, Studies of *Pasteurella pestis* in fleas. VII. The plague-vector efficiency of *Hystrichopsylla linsdalei* compared with *Xenopsylla cheopis* under experimental conditions: American Journal of Tropical Medicine and Hygiene, v. 7, p. 317–322.

Kartman, L., Prince, F.M., Quan, S.F., and Stark, H.E., 1958b, New knowledge of the ecology of sylvatic plague: Annals of the New York Academy of Sciences, v. 70, p. 668–711.

Kartman, L., Quan, S.F., and Lechleitner, R.R., 1962, Die-off of a Gunnison's prairie dog colony in central Colorado. II. Retrospective determination of plague infection in flea vectors, rodents and man: Zoonoses Research, v. 1, p. 201–224.

Keeling, M.J., and Gilligan, C.A., 2000a, Metapopulation dynamics of bubonic plague: Nature, v. 407, p. 903–906.

Keeling, M.J., and Gilligan, C.A., 2000b, Bubonic plague—a metapopulation model of a zoonosis: Proceedings of the Royal Society of London, Series B, v. 267, p. 2219–2230.

Klevytska, A.M., Price, L.B., Schupp, J.M., Worsham, P.L., Wong, J., and Keim, P., 2001, Identification and characterization of variable-number tandem repeats in the *Yersinia pestis* genome: Journal of Clinical Microbiology, v. 39, p. 3179–3185.

Korzun, V.M., and Nikitin, A.I., 1997, Asymmetry of chaetae in fleas *Citellophilus tesquorum* as a possible marker of their capacity for blocking: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 1, p. 34–36.

Kozlov, M., 1979, Plague: natural focality, epizootiology, and epidemic manifestations: Moscow, Meditsina, 192 p.

Kucheruk, V.V., 1965, Paleogenesis of plague natural foci in connection with history of rodent fauna: Fauna i Ekologia Grizunov, v. 7, p. 5–86.

Lechleitner, R.R., Kartman, L., Goldenberg, M.I., and Hudson, B.W., 1968, An epizootic of plague in Gunnison's prairie dogs (*Cynomys gunnisoni*) in south-central Colorado: Ecology, v. 49, p. 734–743.

Lechleitner, R.R., Tileston, J.V., and Kartman, L., 1962, Die-off of a Gunnison's prairie dog colony in central Colorado: Zoonoses Research, v. 1, p. 185–199.

Levi, M.I., 1962, Classification of the varieties of the plague bacillus, *in* Tezisy Dokladov Nauchnoi Konferentsii po Prirodnoi Ochagovosti Chumy i Tularemii, Rostov, p. 72–74.

Levi, M.I., 1994, Gerbils, plague and the Volga (history of one paradox), *in* Levi, M., ed., Zanimatel'nie ocherki o deyatelyah protivochumnoi sistemy Rossii i Sovetskogo Soyuza 1 Informatika: Moscow, Russia, p. 8–44.

Link, V.B., 1955, A history of plague in the United States: U.S. Department of Health, Education and Welfare, Public Health Monograph No. 26, 120 p.

Litvin, V.Y., 1997, Mechanisms of the stable preservation of *Yersinia pestis* in the environment (new facts and hypotheses): Zhurnal Mikrobiologii, issue 4, p. 26–31.

Maevskii, M.P., Bazanova, L.P., and Popkov, A.F., 1999, The survival of the causative agent of plague in the long-tailed suslik from a Tuva natural focus in wintertime: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 1, p. 55–58.

McCoy, G.W., 1908, Plague in ground squirrels: Public Health Reports, v. 23, p. 1289–1293.

Medzykhovsky, G.A., Grazhdanov, A.K., Andryuschenko, V.V., and Tanitovsky, V.A., 2001, The specific features of the spatial and biocenotic structure of a trans-Uralian steppe focus of plague: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 3, p. 39–44.

Mencher, J.S., Smith, S.R., Powell, T.D., Stinchcomb, D.T., Osorio, J.E., and Rocke, T.E., 2004, Protection of black-tailed prairie dogs (*Cynomys ludovicianus*) against plague after voluntary consumption of baits containing recombinant raccoon poxvirus vaccine: Infection and Immunity, v. 72, p. 5502–5505.

Mollaret, H.H., 1963, Conservation expérimentale de la peste dans le sol: Bulletin de la Société Pathologie Exotique, v. 56, p. 1168–1182.

Motin, V.L., Georgescu, A.M., Elliott, J.M., Hu, P., Worsham, P.L., Ott, L.L., Slezak, T.R., Sokhansanj, B.A., Regala, W.M., Brubaker, R.R., and Garcia, E., 2002, Genetic variability of *Yersinia pestis* isolates as predicted by PCR-based IS100 genotyping and analysis of structural genes encoding glycerol-3-phosphate dehydrogenase (glpD): Journal of Bacteriology, v. 184, p. 1019–1027.

Nersesov, V., and Tsikhistavi, G., 1997, On the mechanism of existence of *Yersinia pestis* in nature: Zhurnal Mikrobiologii Moscow, issue 1, p. 102–106.

Nikul'shin, S.V., Onatskaia, T.G., Lukanina, L.M., and Bondarenko, A.L., 1992, Associations of the soil amoeba *Hartmanella rhysodes* with the bacterial causative agents of plague and pseudotuberculosis in an experiment: Zhurnal Mikrobiologii Moscow, issue 9–10, p. 2–5.

Parkhill, J., Wren, B.W., Thomson, N.R., Titball, R.W., Holden, M.T.G., Prentice, M.B., Sebaihia, M., James, K.D., Churcher, C., Mungall, K.L., Baker, S., Basham, D., Bentley, S.D., Brooks, K., Cerdeno-Tarraga, A.M., Chillingworth, T., Cronin, A., Davies, R.M., Davis, P., Dougan, G., Feltwell, T., Hamlin, N., Holroyd, S., Jagels, K., Karlyshev, A.V., Leather, S., Moule, S., Oyston, P.C.F., Quail, M., Rutherford, K., Simmonds, M., Skelton, J., Stevens, K., Whitehead, S., and Barrell, B.G., 2001, Genome sequence of *Yersinia pestis*, the causative agent of plague: Nature, v. 413, p. 523–527.

Parmenter, R.R., Yadav, E.P., Parmenter, C.A., Ettestad, P., and Gage, K.L., 1999, Incidence of plague associated with increased winter-spring precipitation in New Mexico, USA: American Journal of Tropical Medicine and Hygiene, v. 61, p. 814–821.

Perry, R.D., and Fetherston, J.D., 1997, *Yersinia pestis*—etiologic agent of plague: Clinical Microbiology Reviews, v. 10, p. 35–66.

Petrov, V.S., 1959, Natural foci of plague in Eurasia and the principles of their typification: Trudy Sredneaziatskogo Nauchno-Issledovatel'skogo Protivochumnogo Instituta, Alma-Ata, v. 6, p. 3–12.

Petrunina, O.M., 1951, A course of plague infection in great gerbils (*Rhombomys opimus* Licht.) under experimental inoculation: Trudy Sredneaziatskogo Nauchno-Issledovatel'skogo Protivochumnogo Instituta, Alma-Ata, v. 1, p. 17–25.

Poland, J., and Barnes, A., 1979, Plague, *in* Steele, J.H., Stoenner, H., and Kaplan, W., eds., CRC handbook series in zoonoses, Section A—Bacterial, rickettsial, and mycotic diseases, vol. 1: Boca Raton, Fla., CRC Press, p. 515–597.

Poland, J., Quan, T.J., and Barnes, A.M., 1994, Plague, *in* Beran, G.W., ed., CRC handbook series in zoonoses, Section A—bacterial, rickettsial, and mycotic diseases: Boca Raton, Fla., CRC Press, p. 93–112.

Pollitzer, R., 1954, Plague: Geneva, Switzerland, World Health Organization Monograph Series No. 22., 698 p.

Pollitzer, R., 1960, A review of recent literature on plague: Bulletin of the World Health Organization, v. 23, p. 313–400.

Pollitzer, R., and Meyer, K.F., 1961, The ecology of plague, *in* May, J.F., ed., Studies of disease ecology: New York, Hafner, p. 433–501.

Prentice, M.B., James, K.D., Parkhill, J., Baker, S.G., Stevens, K., Simmonds, M.N., Mungall, K.L., Churcher, C., Oyston, P.C.F., Titball, R.W., Wren, B.W., Wain, J., Pickard, D., Hien, T.T., Farrar, J.J., and Dougan, G., 2001, *Yersinia pestis* pFRa shows biovar-specific differences and recent common ancestry with a *Salmonella enterica* serovar typhi plasmid: Journal of Bacteriology, v. 183, p. 2586–2594.

Pushkareva, V.I., 2003, Experimental evaluation of interactions between *Yersinia pestis* EV and soil infusoria and the possibility of the prolonged preservation of bacteria in the protozoan cysts: Zhurnal Mikrobiologii Moscow, issue 4, p. 40–44.

Quan, S.F., Burroughs, A.L., Holdenried, R., and Meyer, K.F., 1953, Studies on the prevention of experimental plague epizootics instituted among mice by infected fleas: Atti del VI Congresso Internazionale di Microbiologia Roma, v. 5, p. 537–540.

Quan, S.F., and Kartman, L., 1956, The resistance of *Microtus* and *Peromyscus* to infection by *Pasteurella pestis*: Transactions of the Royal Society of Tropical Medicine and Hygiene, v. 50, p. 104–105.

Rall, Y.M., 1965, Natural focality and epizootiology of plague: Moscow, Medgiz, 338 p.

Rayor, L.S., 1985, Dynamics of a plague outbreak in Gunnison's prairie dog: Journal of Mammalogy, v. 66, p. 194–196.

Rivkus, Y.Z., Mitropolsky, O.V., Bochkaroff, V.M., Blummer, A.G., and Bochkaroff, S.V., 1993, Desert vegetation as a possible component in plague parasitocoenosis: Bulleten Moskovskogo Obschestva Ispytatelei Prirody, v. 98, p. 3–13.

Rivkus, Y., Ostrovskii, I., Melnikov, I., and Dyatlov, A., 1973, On sensitivity to plague in *Rhombomys opimus* from the northern Kizil-Kum: Problemy Osobo-opasnih Infektsii, Saratov, v. 30, p. 48–58.

Rocke, T.E., Mencher, J., Smith, S.R., Friedlander, A.M., Andrews, G.P., and Baeten, L.A., 2004, Recombinant F1-V fusion protein protects black-footed ferrets (*Mustela nigripes*) against virulent *Yersinia pestis* infection: Journal of Zoo and Wildlife Medicine, v. 35, p. 142–146.

Rotshild, E.V., 2001, Relationship between infectious diseases and concentration of trace metals in the environment and periodic law: Uspehi Sovremennoi Biologii (Moscow), v. 121, p. 251–265.

Seery, D.B., Biggins, D.E., Montenieri, J.A., Enscore, R.E., Tanda, D.T., and Gage, K.L., 2003, Treatment of black-tailed prairie dog burrows with deltamethrin to control fleas (Insecta: Siphonaptera) and plague: Journal of Medical Entomology, v. 40, p. 718–722.

Serzhanov, O.S., Aubakirov, S.A., Ageev, V.S., Matakov, M.I., and Chervyakov, V.D., 1982a, Use of hydrological characteristics for search of places with stable enzootic activity of plague: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 3, p. 80–84.

Serzhanov, O.S., Aubakirov, S.A., Fomushkin, V.M., Ageev, V.S., and Turkpenbaev, H., 1982b, Classification of Central Asian desert plague foci by using hydrothermal indices: Meditsinskaya Parazitologiya i Parazitarnye Bolezni (Moscow), issue 4, p. 46–50.

Sharets, A.S., Berendyayev, S.A., Krasnikova, L.V., and Tristan, D.F., 1958, The epizootiological effectiveness of one-shot extermination of marmots: Trudy Sredneaziatskogo Nauchno-Issledovatel’skogo Protivochumnogo Instituta, Alma-Ata, v. 4, p. 145–147.

Song, Y., Tong, Z., Wang, J., Wang, L., Guo, Z., Han, Y., Zhang, J., Pei, D., Zhou, D., Qin, H., Pang, X., Han, Y., Zhai, J., Li, M., Cui, B., Qi, Z., Jin, L., Dai, R., Chen, F., Li, S., Ye, C., Du, Z., Lin, W., Wang, J., Yu, J., Yang, H., Wang, J., Huang, P., and Yang, R., 2004, Complete genome sequence of *Yersinia pestis* strain 91001, an isolate avirulent to humans: DNA Research, v. 11, p. 179–197.

Stapp, P., Antolin, M.F., and Ball, M., 2004, Patterns of extinction in prairie-dog metapopulations—plague outbreaks follow El Nino events: Frontiers in Ecology and the Environment, v. 2, p. 235–240.

Stepanov, V.M., 1975, Nutrition factors and their role in manifestation of virulence and immunogenicity of plague pathogen: Saratov, Mikrob Institute Press, 285 p.

Suchkov, I.G., Khidiakov, I.V., Emel’ianenko, E.N., Levi, M.I., Pushkraeva, V.I., Suchko, I.I., Litvin, V., Kulesh, E.V., Zotova, R.S., and Gintsburg, A.L., 1997, The possibility of preserving the causative agent of plague in soil in resting (nonculturable) form: Zhurnal Mikrobiologii, Epidemiologii i Immunobiologii, issue 4, p. 42–46.

Suleimenov, B.M., 2004, Mechanism of plague enzooticity: Almaty, Kazakhstan, Aikembayev’s Scientific Center for Quarantinable and Zoonotic Diseases, 234 p.

Suntsov, V.V., and Suntsova, N.I., 2000, Ecological aspects of the evolution of the plague microbe *Yersinia pestis* and the genesis of natural foci: Izvestiya Akademii Nauk, Seriya Biologicheskaya, issue 6, p. 645–657.

Thomas, R.E., Barnes, A.M., Quan, T.J., Beard, M.L., Carter, L.G., and Hopla, C.E., 1988, Susceptibility to *Yersinia pestis* in the northern grasshopper mouse (*Onychomys leucogaster*): Journal of Wildlife Diseases, v. 24, p. 327–333.

Tikhomirov, E., 1999, Epidemiology and distribution of plague, *in* Plague manual: Geneva, Switzerland, World Health Organization, p. 11–41.

Trebesius, K., Harmsen, D., Rakin, A., Schmelz, J., and Heesemann, J., 1998, Development of rRNA-targeted PCR and in situ hybridization with fluorescently labelled oligonucleotides for detection of *Yersinia* species: Journal of Clinical Microbiology, v. 36, p. 2557–2564.

Trudeau, K.M., Britten, H.B., and Restani, M., 2004, Sylvatic plague reduces genetic variability in black-tailed prairie dogs: Journal of Wildlife Diseases, v. 40, p. 205–211.

Tumanskii, V.M., 1957, Classification of the varieties of *P. pestis*: Zhurnal Mikrobiologii Moscow, v. 28, p. 3–7.

Tumanskii, V.M., 1958, Mikrobiologiia chumy (Microbiology of plague) (2d ed.): Moscow, Medgiz.

Ubico, S.R., Maupin, G.O., Fagerstone, K.A., and McLean, R.G., 1988, A plague epizootic in the white-tailed prairie dogs (*Cynomys leucurus*) of Meeteetse, Wyoming: Journal of Wildlife Diseases, v. 24, p. 399–406.

Voronova, G.A., 1989, Enhanced blocking capability of plague microbe in the body of flea: Parazitologiya, v. 23, p. 427–429.

Williams, J.E., and Cavanaugh, D.C., 1983, Chronic infections in laboratory rodents from inoculation of non-encapsulated plague bacilli (*Yersinia pestis*): Experientia, v. 39, p. 408–409.

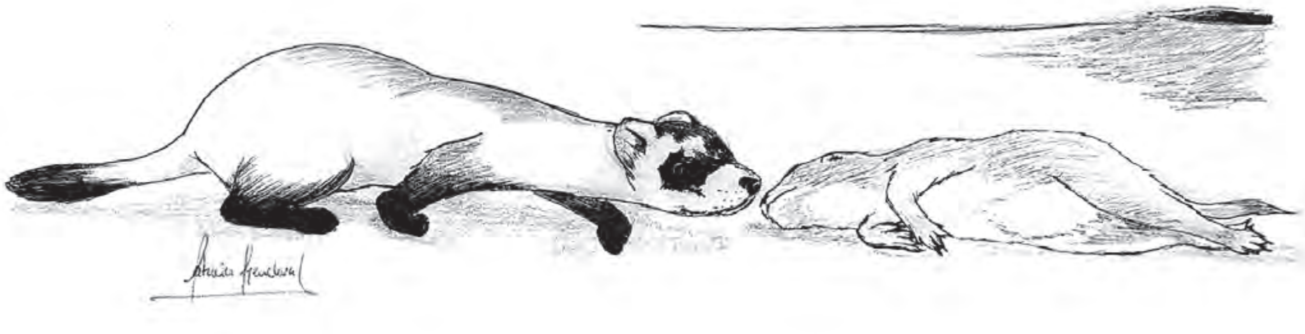
Williams, J.E., Harrison, D.N., and Cavanaugh, D.C., 1975, Cryptic infection of rats with non-encapsulated variants of *Yersinia pestis*: Transactions of the Royal Society of Tropical Medicine and Hygiene, v. 69, p. 171–172.

Williams, E.S., Mills, K., Kwiatkowski, D.R., Thorne, E.T., and Boerger-Fields, A., 1994, Plague in a black-footed ferret (*Mustela nigripes*): Journal of Wildlife Diseases, v. 30, p. 581–585.

World Health Organization, 2004, Human plague in 2002 and 2003: Weekly Epidemiological Record, v. 79, p. 301–306.

Wren, B.W., 2003, The yersiniae—a model genus to study the rapid evolution of bacterial pathogens: Nature Reviews Microbiology, v. 1, p. 55–64.

Zabolotny, D.K., 1915, Pulmonary plague in 1910–1911: Petrograd, Accounts of the Russian Scientific Expedition, 1915.



Exposure of Captive Black-footed Ferrets to Plague and Implications for Species Recovery

By Jerry L. Godbey,[1] Dean E. Biggins,[1] and Della Garelle[2]

Abstract

Plague, a disease caused by the bacterium *Yersinia pestis*, was introduced into North America ca. 1900 and is now common within the ranges of three species of prairie dogs (*Cynomys* spp.) that collectively composed the former range of the highly endangered black-footed ferret (*Mustela nigripes*). An experimental population of black-footed ferrets living in quasi-natural outdoor pens suffered 90 percent mortality after they ate prairie dogs infected with *Y. pestis*. Lethal and sublethal exposure of Siberian polecats (*Mustela eversmannii*) subsequently released into those pens suggested that live *Y. pestis* can be maintained in animal tissues within burrow systems for at least 2 months. A combination of low levels of prairie dog mortality and persistence of *Y. pestis* in dead hosts may pose a chronic hazard for free-ranging black-footed ferrets in areas where plague is enzootic.

Keywords: black-footed ferret, disease, introduced disease, invasive species, *Mustela eversmannii*, *Mustela nigripes*, plague, Siberian polecat, *Yersinia pestis*.

Background

Plague was once believed to be millions of years old, but recent genetic evidence suggests that the causative bacterium, *Yersinia pestis*, may have evolved from *Y. pseudotuberculosis* only 1,500–20,000 years ago (Achtman and others, 1999). The disease has caused devastating epidemics in humans. Plague-like symptoms were recorded in human populations of Asia and Africa as early as 541 A.D. Most scientists believe that plague was introduced into North America from Asia in the late 19th century via rats (*Rattus* spp.) transported by ships (Biggins and Kosoy, 2001). There is now evidence of plague infection in wild mammals or fleas (Insecta: Siphonaptera) from 17 western States in the United States (Gage and Kosoy, this volume).

There are multiple transmission modes for plague, including vector transport (flea bites), aerosol, and consumption of contaminated food items (Gage and Kosoy, this volume). Early cases of plague were linked with rodent infestations and assumed to be from rodent bites, but it was soon recognized that fleas could spread the disease among hosts (Gage, 1998). Aerosol transmission involves expulsion of contaminated droplets of fluid from the lungs of infected animals as they cough; the droplets containing *Y. pestis* may be ingested or inhaled by another potential host. Transmission has also been documented through consumption of infected animals (Gage and Kosoy, this volume). Although some carnivores become infected and do not survive, other species seem quite resistant (Barnes, 1982; Gage and others, 1995).

Plague is common within the ranges of three species of prairie dogs (*Cynomys* spp.) that collectively composed the former range of the highly endangered black-footed ferret (*Mustela nigripes*). The black-footed ferret is extremely dependent on prairie dogs and their colonies (Biggins and Godbey, 2003). Plague causes periodic and sometimes dramatic die-off of prairie dogs, indirectly affecting ferret survival through reduction of prey biomass (Oldemeyer and others, 1993). In 1985, discovery of plague in the white-tailed prairie dogs (*C. leucurus*) supporting the last known population of wild ferrets in Meeteetse, Wyo. (Ubico and others, 1988), caused great concern about the future of ferret habitat. White-tailed prairie dogs were found to be highly susceptible to the disease, but susceptibility of the black-footed ferret was unknown (Williams, 1986). The fears of habitat loss and an unstable prey base proved well founded. A 10-year decline in prairie dogs at Meeteetse left only a remnant population. The initial steep decline of prairie dogs at Meeteetse (fig. 1) was accompanied by a decline in ferrets, which may have been exacerbated by a second disease, canine distemper (Forrest and others, 1988). The dramatic ferret population decline

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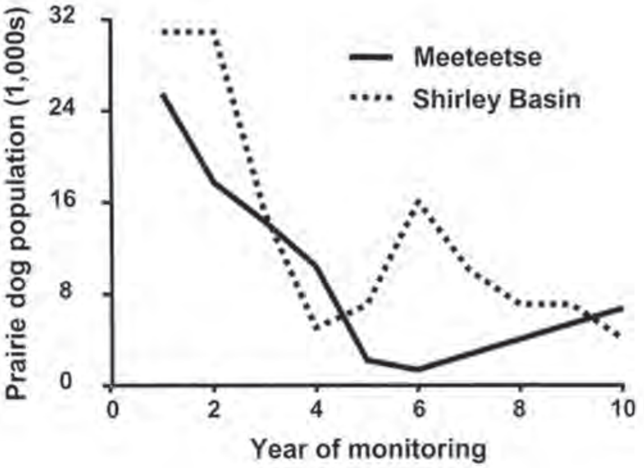

Figure 1. Changes in Wyoming white-tailed prairie dog (*Cynomys leucurus*) populations in areas with known plague. (Adapted from Biggins and Kosoy, 2001. Reprinted with permission of the *Journal of the Idaho Academy of Science*, Pocatello, Idaho.)

prompted the capture of remaining ferrets for captive breeding (Biggins and others, 1997).

The captive breeding program to produce animals for reintroduction into native habitat (i.e., complexes of prairie dog colonies) was ultimately successful (Biggins and Godbey, 2003). Reintroductions of ferrets were begun in 1991 into Wyoming white-tailed prairie dog colonies at Shirley Basin where plague was known to be established. The Shirley Basin population of prairie dogs also declined (fig. 1), but more recently the population has shown some signs of recovery. In 1994, releases of ferrets began in a Montana black-tailed prairie dog (*C. ludovicianus*) complex also known to have plague. Plague has been documented at most reintroduction or potential reintroduction sites, with the exception of those in South Dakota, throughout the ferret range.

Plague was not believed to be a direct hazard to ferrets at the time of the first reintroductions. Williams and others (1991) initially reported that domestic ferrets (*Mustela putorius furo*) and Siberian polecats (*Mustela eversmannii*) were resistant to plague and suggested that “concern about black-footed ferret mortality directly due to *Y. pestis* infection is probably not warranted.” It was therefore surprising to hear of the death of a black-footed ferret due to plague infection (Williams and others, 1994). Williams’s further work with black-footed ferret × Siberian polecat hybrids provided additional evidence on the direct hazard of plague. Nine of 12 hybrids tested became infected and died from ingestion of plague-killed mice; the three survivors failed to show an antibody response (E. Williams, oral commun., 1996). A subsequent trial resulted in 100 percent mortality of four black-footed ferrets exposed to about 800 organisms (equivalent to one flea bite dose) of *Y. pestis* by subcutaneous injection (E. Williams, oral commun., 1999).

Plague Exposure of Captive Black-footed Ferrets at Pueblo

On November 19, 1995, an experimental colony of black-footed ferrets was inadvertently exposed to plague at a research facility housed at the U.S. Army’s Pueblo Chemical Depot, Pueblo, Colo. The facility consisted of modified buildings and enclosures that provided quasi-natural environments for rearing and conditioning black-footed ferrets prior to release. Indoor cages and outdoor pens of various sizes were also used. Outdoor pens consisted of earth-filled structures (fig. 2) with combinations of natural burrows dug by prairie dogs, seminatural burrows constructed of 10.2-cm corrugated plastic drain pipe buried to a depth of about 1 m, and nest boxes. Studies on ferret behaviors were being conducted by using Siberian polecats, black-footed ferrets, and domestic ferrets reared in various environments. There were 64 resident black-footed ferrets in three categories at the time of the exposure. Twenty-three ferrets were assigned to the behavioral studies. Twenty-six ferrets had just been received and were being conditioned as experimental groups for release in Arizona and Montana. Fifteen ferrets 4−7 years old were being held awaiting transfer to zoos as display animals. Most of the black-footed ferrets were provided a diet of prairie dog portions on alternating days; Siberian polecats and domestic ferrets were fed commercial mink chow. The prairie dogs were live-trapped from various sources, quarantined for 10 days, sacrificed, and then frozen until used.

Thirty ferrets were fed on November 19, 1995. The food included portions from five quarantined black-tailed prairie dogs originating in Montana that were removed from one freezer and two nonquarantined Gunnison’s prairie dogs (*C. gunnisoni*) captured from a site near Cortez, Colo., in August

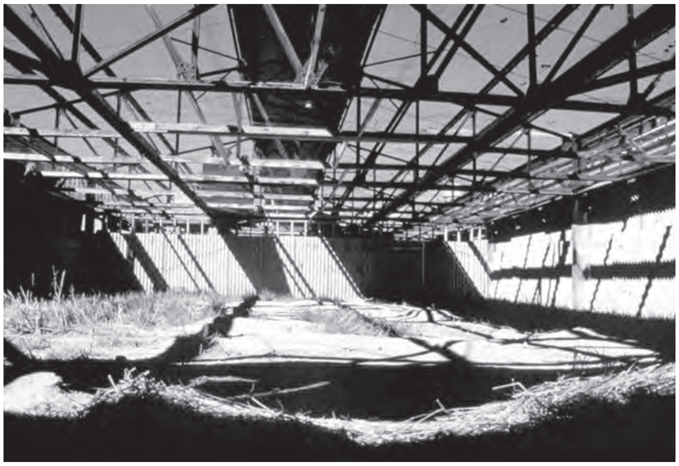

Figure 2. Black-footed ferrets (*Mustela nigripes*) occupied complex burrow systems dug by prairie dogs (*Cynomys* spp.), making them difficult or impossible to locate during and after the outbreak of plague.

1994 and stored in a second freezer. Only the Montana prairie dogs were to be fed, but new animal care personnel were unaware of the distinction. All seven prairie dogs were cut into large pieces on a common cutting board and placed into a bowl for transport to the pens.

Two days after feeding (November 21, 1995), the crew discovered the first obviously ill black-footed ferret in an outdoor pen. The ferret died soon after it was captured. Food-borne disease or poisoning was immediately suspected, so the remaining food was removed, the facilities were quarantined for 10 days, and vitamin K was administered to counteract possible rodenticide poisoning. Ten uneaten or partially eaten pieces of prairie dog were found. Black-tailed and Gunnison's prairie dog parts could not be distinguished because the skin had been removed. The recovered food and the bowl were sent to the Centers for Disease Control (CDC) in Fort Collins, Colo., for testing. Several whole prairie dogs from the Montana shipment and two Gunnison's prairie dogs remaining in the second freezer were also sent to the CDC. Repeated searches of the pens over the next 2 days disclosed other sick and dead ferrets. Clinical signs included lethargy and bloody stools. Of the 30 animals possibly exposed, 19 died and 8 were missing and presumed dead in underground burrows. Black-footed ferret remains were sent to Colorado State University for necropsy, and tissue samples were forwarded to the CDC for plague testing. The three surviving animals were quarantined, and blood was drawn and sent to the CDC.

Three of the 10 recovered prairie dog pieces, the two remaining Gunnison's prairie dogs, and a swab taken from the inner surface of the transport bowl tested positive for plague. There was no evidence of plague in the tested Montana black-tailed prairie dogs. All dead ferrets were positive for plague in one or more tissue samples. Internal organs showed various stages of infection, but all included intestinal hemorrhaging and congested lungs. Clinical signs were consistent with advanced stages of plague.

Labels on recovered freezer bags indicated that the two Gunnison's prairie dogs fed to the ferrets had died during capture or shipment. During 1994 and 1995, former technicians working at the Pueblo facility received several shipments of Gunnison's prairie dogs from Mr. Gay Balfour of Dog Gone, Inc., Cortez, Colo. Mr. Balfour used a modified industrial street cleaning machine with a large vacuum to extract live prairie dogs from their burrows. A small percentage of his catch was injured or killed during capture, and a few prairie dogs may have been dead in the burrow when extracted by the vacuum. These nonquarantined prairie dogs were to be tested later for plague and stored separately from quarantined prairie dogs. One or both of the Gunnison's prairie dogs fed to the ferrets was likely infected with *Y. pestis*. It is unlikely that all 30 black-footed ferrets received Gunnison's prairie dog pieces. We believe the infected portions of Gunnison's prairie dog cross-contaminated the rest of the prairie dog pieces during processing on the cutting board and/or while being carried in the transport bowl.

Surviving ferret #1148 shared a pen with another black-footed ferret (#268) that died from plague. Initial serum samples from #1148 (December 14, 1995) showed no evidence of plague exposure as judged by passive hemagglutination assay; however; surviving ferrets #565 (titer 1:128) and #1508 (titer 1:256) did show evidence of exposure (fig. 3). Ferrets #1508 and #1148 were transferred to reintroduction sites (Montana and Arizona, respectively) before additional blood samples could be taken. Ferret #565 remained at Pueblo, and blood samples were taken at 2-week intervals to follow the immune response. The titer level for ferret #565 increased to 1:2,048 and then diminished to 1:64 over the next 5 months (fig. 3).

Questions arose regarding the persistence of plague underground, and we elected to move some of the resident Siberian polecats from cages to the outdoor pens for exposure testing. On January 23, 1996, 11 male-female pairs of polecats were transferred into pens that had held ferrets that either died or disappeared. We radio tagged the polecats and took baseline serum samples prior to the transfer. Polecats were located each day visually or via radio telemetry. Additional blood samples were taken approximately monthly for 5 months, and irregularly thereafter.

On January 28, 1996, polecat #889 was found dead underground via radio telemetry. Necropsy and tests of tissues indicated plague as the cause of death. The pen had previously housed a black-footed ferret (#1410) whose body was not recovered. On February 13, 1996, polecat #800 carried the partially mummified remains of a formerly missing black-footed ferret (#1471) into a nest box. Subsequent tests of the polecat's blood indicated no evidence of exposure to plague; however, the remains of ferret #1471 were positive for plague.

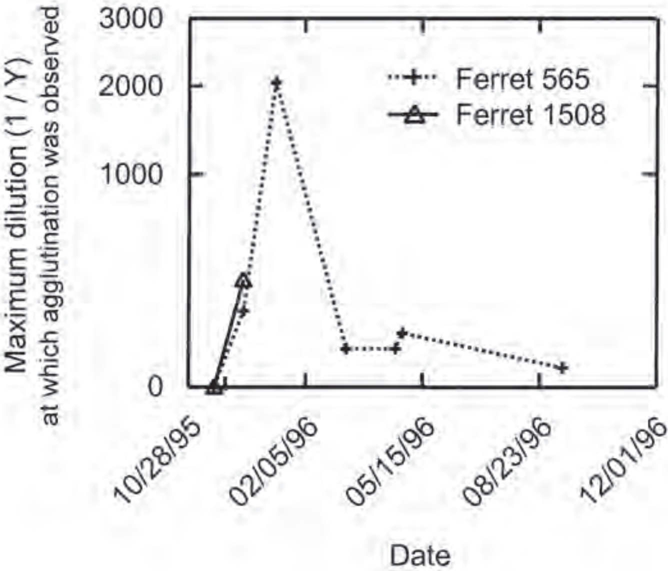

Figure 3. Antibody responses (as determined by passive hemagglutination) of black-footed ferrets (*Mustela nigripes*) #1508 and #565. Estimated date of exposure was 11/19/1995.

On February 23, 1996, polecat #094 recovered the remains of black-footed ferret #636. Serum samples indicated that polecat #094 was positive for plague and remained so for more than 3 months without clinical symptoms (fig. 4). The recovered body of black-footed ferret #636 also tested positive for plague. Siberian polecat #293, housed in a pen where ferret #526 had disappeared, also tested positive for plague. Thus, of the 22 polecats moved to the black-footed ferret pens, 3 tested positive for plague, 1 of which died. One of the seropositive surviving polecats was likely exposed when it recovered the remains of a plague-positive ferret. However, an additional polecat that recovered a plague-positive ferret tested negative. The remaining 18 polecats, including the pen mates of the three that were seropositive for plague, tested negative.

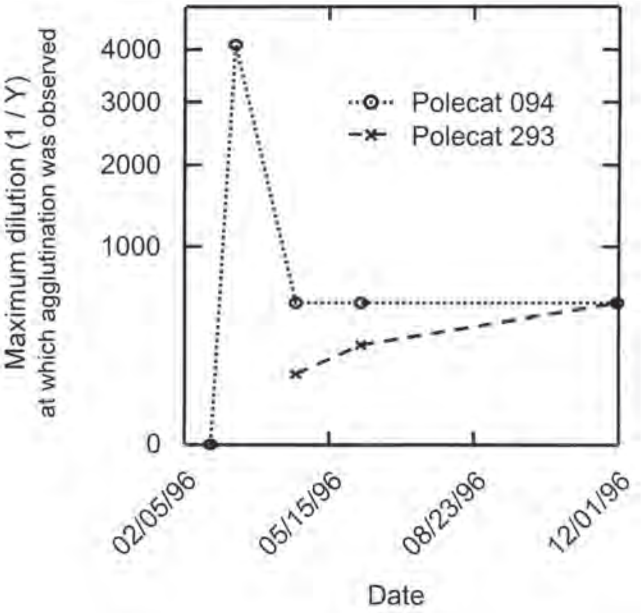

Figure 4. Antibody responses (as determined by passive hemagglutination) of two Siberian polecats (*Mustela eversmannii*) exposed to plague. Earliest potential date of exposure was 1/23/1996, when polecats were moved into pens.

Discussion

Black-footed ferrets may die within 48 hours of consuming plague-infected meat. Of the 30 animals in the group potentially exposed, 27 likely died (some were missing), and 3 survived (2 with antibody responses and 1 with no seroconversion even though its pen mate died of plague). This high rate of mortality was surprising given the circumstances of exposure. Some ferrets apparently ate prairie dog pieces that were surface-contaminated (by mixing with other pieces from infected prairie dogs) and probably received a fairly low dose of *Y. pestis.* Perhaps the two ferrets that survived exposure and showed antibody response consumed very low numbers of bacteria.

Black-footed ferrets are known to scavenge opportunistically; that habit, combined with the fact that plague has been repeatedly detected at most of the black-footed ferret reintroduction sites, suggests that plague-killed rodents constitute a real and eminent hazard for free-ranging black-footed ferrets. Because of the persistence of live *Y. pestis* in carcasses for more than 2 months in relatively cool and humid prairie dog burrows, the hazard may linger long after an epizootic has killed the rodents. If *Y. pestis* resides in prairie dog colonies, occasionally causing disease in individual prairie dogs or other rodents, the risk posed by even widely spaced carcasses could be serious for the relatively mobile foraging ferrets.

Although titers of the Siberian polecats declined, they remained sufficiently high during the course of monitoring (ca. 1 year) to suggest immunity to plague (fig. 4). Because the native habitats of Siberian polecats are centered on Asian foci of plague, these polecats were hypothesized to be more resistant than black-footed ferrets to the disease. Nevertheless, plague killed 88 percent of 33 polecats exposed to *Y. pestis* through subcutaneous injections and consumption of plague-killed mice (Castle and others, 2001), a loss rate similar to the suspected mortality rate for black-footed ferrets (90 percent) in the Pueblo incident.

The initial plague exposure of ferret #565 was more than 3 weeks before the first blood sample was taken on December 14, 1995. The greatest measured antibody response (1:2,048) was on January 11, 1996 (fig. 3), followed by a decline. The relatively low titers after just 3 months may have been insufficient to confer protection against subsequent exposure to plague (fig. 3). Consequently, long-term protection against plague via vaccination may be problematic in black-footed ferrets. More research is clearly needed.

It is unlikely that plague can be eliminated from the wild in North America. Protection of the black-footed ferret from this disease may depend in part on the ability to reduce its spread among and within prairie dog colonies and complexes. The use of pesticides to reduce flea populations provides some hope of reducing plague outbreaks and stabilizing treated areas (Durbian and others, 1997; Karhu and Anderson, 2000; Seery and others, 2003). Repeated dusting of burrows with pesticides, however, is labor intensive and perhaps not practical for large colonies and complexes. If a management tool (e.g., insecticide) can eliminate plague from a prairie dog colony, both ferrets and prey will be afforded some protection. Initial results suggest that flea control may reduce or eliminate epizootics of plague on prairie dog colonies but may not eliminate *Y. pestis* completely. If low levels of enzootic plague remain on such colonies, the threat to ferrets may be substantial, and additional management intervention (e.g., vaccination of ferrets) may be necessary.

Plague is currently common throughout the majority of the black-footed ferret's historical range. Remaining plague-free areas have become vital to reestablishment of the ferret. Why some prairie dog complexes are plague free and how long they will remain so are unknowns. The few remaining plague-free areas provide a unique opportunity to learn about black-footed ferret habitat before plague becomes endemic. As experimental reintroductions and plague research continue, special consideration should be given to existing plague-free areas for recovering the black-footed ferret and for increasing our knowledge of plague dynamics through comparisons of areas with and without the disease.

References Cited

Achtman, M., Zurth, K., Morelli, G., Torrea, G., Guiyoule, A., and Carniel, E., 1999, *Yersinia pestis*, the cause of plague, is a recently emerged clone of *Yersinia pseudotuberculosis*: Proceedings of the National Academy of Sciences, v. 96, p. 14043–14048.

Barnes, A.M., 1982, Surveillance and control of bubonic plague in the United States: Symposia of the Zoological Society of London, v. 50, p. 237–270.

Biggins, D.E., and Godbey, J.L., 2003, Challenges to reestablishment of free-ranging populations of black-footed ferrets: Comptes Rendus Biologies, v. 326 (Suppl. 1), p. S104–S111.

Biggins, D.E., and Kosoy, M.Y., 2001, Influences of introduced plague on North American mammals—implications from ecology of plague in Asia: Journal of Mammalogy, v. 82, p. 906–916.

Biggins, D.E., Miller, B.J., Clark, T.W., and Reading, R.P., 1997, Management of an endangered species: the black-footed ferret, *in* Meffe, G., and Carroll, R., eds., An introduction to conservation biology (2d ed.): Sunderland, Mass., Sinauer Associates, Inc., p. 420–426.

Castle, K.T., Biggins, D.E., Carter, L.G., Chu, M., Innes, K., and Wimsatt, J., 2001, Susceptibility of the Siberian polecat to subcutaneous and oral *Yersinia pestis* exposure: Journal of Wildlife Diseases, v. 37, p. 746–754.

Durbian, F.E., III, Dullum, J., and Matchett, R., 1997, Summary of the 1997 prairie dog flea dusting effort on the Charles M. Russell and UL Bend National Wildlife Refuges and adjacent Bureau of Land Management lands: Lewistown, Mont., U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, 6 p.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.

Gage, K.L., 1998, Plague, *in* Collier, L., Balows, A., Sussman, M., and Hausler, W.J., Jr., eds., Topley and Wilson's microbiology and microbial infections (9th ed.), vol. 3, Bacterial infections: London, Arnold, p. 885–904.

Gage, K.L., Ostfeld, R.S., and Olson, J.G., 1995, Nonviral vector-borne zoonoses associated with mammals in the United States: Journal of Mammalogy, v. 76, p. 695–715.

Karhu, R.R., and Anderson, S.H., 2000, Effects of pyriproxyfen spray, powder, and oral bait treatments on the relative abundance of fleas (Siphonaptera: Ceratophyllidae) in black-tailed prairie dog (Rodentia: Sciuridae) towns: Journal of Medical Entomology, v. 37, p. 864–871.

Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., 1993, Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, 96 p.

Seery, D.B., Biggins, D.E., Montenieri, J.A., Enscore, R.E., Tanda, D.T., and Gage, K.L., 2003, Treatment of black-tailed prairie dog burrows with deltamethrin to control fleas (Insecta: Siphonaptera) and plague: Journal of Medical Entomology, v. 40, p. 718–722.

Ubico, S.R., Maupin, G.O., Fagerstone, K.A., and McLean, R.G., 1988, A plague epizootic in the white-tailed prairie dogs (*Cynomys leucurus*) of Meeteetse, Wyoming: Journal of Wildlife Diseases, v. 24, p. 399–406.

Williams, E.S., 1986, Experimental infection of white-tailed prairie dogs (*Cynomys leucurus*) with plague (*Yersinia pestis*): Preliminary report to the U.S. Fish and Wildlife Service, Fort Collins, Colo., 11 p.

Williams, E.S., Mills, K., Kwiatkowski, D.R., Thorne, E.T., and Boerger-Fields, A., 1994, Plague in a black-footed ferret (*Mustela nigripes*): Journal of Wildlife Diseases, v. 30, p. 581–585.

Williams, E.S., Thorne, E.T., Quan, T.J., and Anderson, S.L., 1991, Experimental infection of domestic ferrets (*Mustela putorius furo*) and Siberian polecats (*M. eversmanni*) with *Yersinia pestis*: Journal of Wildlife Diseases, v. 27, p. 441–445.

Use of Pesticides To Mitigate the Effects of Plague

By David B. Seery[1,2]

Abstract

On several occasions from 1989 to 2002, burrows within black-tailed prairie dog (*Cynomys ludovicianus*) towns on the Rocky Mountain Arsenal National Wildlife Refuge, Colo., were dusted with a variety of insecticides (carbaryl, permethrin, and deltamethrin) to reduce flea (Insecta: Siphonaptera) abundance in attempts to control plague epizootics. Prairie dog populations were monitored with a combination of various mapping techniques and population abundance indices (visual counts). A single application of deltamethrin significantly reduced populations of the plague vector *Oropsylla hirsuta* and other flea species on prairie dogs and in prairie dog burrows for at least 84 days. A plague epizootic on the Rocky Mountain Arsenal National Wildlife Refuge caused high mortality of prairie dogs on some untreated towns but did not appear to affect nearby towns dusted with deltamethrin. Large-scale relocation efforts followed plague epizootics during the late 1980s and 1990s in an effort to rebuild populations to support wintering eagles and hawks. Between 1989 and 2002, the U.S. Fish and Wildlife Service relocated 12,692 prairie dogs at the Refuge. A comprehensive population monitoring program was instituted in the early 1990s to gage the effectiveness of plague control and relocation. This paper presents a summary of the plague control, relocation, and population monitoring program.

Keywords: black-tailed prairie dog, *Cynomys ludovicianus*, deltamethrin, permethrin, pesticide, plague, *Yersinia pestis*

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) have been intensively managed at the U.S. Fish and Wildlife Service's (FWS) Rocky Mountain Arsenal National Wildlife Refuge (Refuge) since 1986, when a significant bald eagle (*Haliaeetus leucocephalus*) communal winter roost was discovered. Wintering bald eagles feed largely on prairie dogs, through kleptoparasitism of ferruginous hawk (*Buteo regalis*) predations (U.S. Fish and Wildlife Service, 1990). At the Refuge, prairie dogs also provide habitat for burrowing owls (*Athene cunicularia*) and grassland birds, and prey for coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and several species of hawks.

The Refuge is located approximately 16 km northeast of downtown Denver, Colo. Beginning in 1942, the U.S. Army used the site to manufacture chemical and incendiary weapons. After World War II, private companies leased the industrial site for the manufacture of pesticides and herbicides. The Refuge was designated as a Superfund site in 1986 and is currently undergoing environmental remediation. Congress passed legislation in 1992 that established the Refuge upon completion of environmental cleanup. The legislation also states that the Refuge will be managed as if it were a national wildlife refuge during the cleanup. The data collected and analyzed here are part of a larger-scale effort to characterize populations of wildlife at the Refuge. The Refuge currently covers over 6,900 ha in a mosaic of habitat types, including wetland, riparian, and various types and successional stages of grasslands.

Plague (*Yersinia pestis* infection) has periodically affected prairie dog towns on the Refuge since the 1970s. Efforts to control plague during past epizootics involved insecticides, including carbaryl and permethrin dust to control fleas (Insecta: Siphonaptera). Most early efforts were conducted primarily in the interest of public health rather than specifically to protect prairie dogs as important habitat for wildlife species.

Large-scale relocation efforts followed plague epizootics during the late 1980s and 1990s in an effort to rebuild populations to support wintering eagles and hawks. A comprehensive population monitoring program was instituted in the early 1990s to gage the effectiveness of the plague control and relocation program. This paper presents a summary of the plague control, relocation, and population monitoring program, which included mapping active prairie dog colony distribution and visual counts.

Monitoring Distribution and Abundance of Prairie Dogs

Prairie dog colony distribution was determined by using aerial photo interpretation and field verification in all surveys conducted from 1988 to 1993 (Ebasco Services, Inc., 1989; U.S. Fish and Wildlife Service, 1994). Black and white section

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photographs with a scale of approximately 1 cm = 79.2 m were used as field reference guides. Frosted mylar was placed over each section photo, and the boundaries of prairie dogs towns were delineated in the field. Only active prairie dog towns were included in the survey. Mapping was usually conducted in the spring after emergence of prairie dog litters, with some additional mapping at other times of the year to document changes due to plague. Upon completion of the field mapping, the area of each town was determined by using a Radian's Contour Plotting System-1 (CPS-1) for the 1988–90 surveys and an electronic planimeter for the 1991–93 surveys.

Prairie dog town distribution was mapped from 1994 to 2002 by using a TDC1 Global Positioning System (GPS) unit and Pathfinder® software (Trimble Navigation, Ltd., Sunnyvale, Calif.). GPS positions were collected by walking the perimeters of active prairie dog towns and recording positions at 10 to 15 second intervals. The perimeters were determined by outermost active prairie dog burrows or by vegetation clipping (where obvious). GPS data files collected and stored in the rover unit were then downloaded to a computer for subsequent differential analysis. Differential correction (to increase accuracy to 2–5 m) was completed by using community base station files downloaded locally or from the U.S. Forest Service in Fort Collins, Colo. Areas of prairie dog towns were then determined by using Pathfinder software. Final maps were developed with ArcView® software (Environmental Systems Research Institute, Inc., Redlands, Calif.).

Visual counts have been used to estimate populations of white-tailed prairie dogs (*Cynomys leucurus*) and Richardson's ground squirrels (*Spermophilus richardsonii*) and have been shown to correlate well with estimates obtained from mark-recapture data from the same sites (Fagerstone, 1983; Fagerstone and Biggins, 1986; Menkins and others, 1990). Visual counts were chosen as the primary method to estimate population density of black-tailed prairie dogs on the Refuge. This methodology was developed by the FWS's National Ecology Research Center (now the Fort Collins Science Center, U.S. Geological Survey) in Fort Collins, Colo., to evaluate black-footed ferret habitat (Biggins and others, 1993). Study plots of various sizes were established (depending on time, personnel, and suitability of habitat constraints), and in some cases entire prairie dog towns were counted. Visual counts were conducted for 3 consecutive days on each plot, starting approximately 30 minutes after sunrise and continuing (with 15 minutes between counts) until prairie dog numbers began to decrease, usually midmorning. The highest individual count of prairie dogs recorded during the 3 days was then used to determine the density of each plot (highest count/area). Densities were then summed and divided by the number of plots to determine the mean density for each year.

History of Plague at the Refuge

Early efforts to control plague at the Refuge began in the mid-1970s. Carbaryl insecticide was infused into prairie dog burrows in an effort to control fleas and the spread of plague in the central portion of the Refuge. Primary attention was given to prairie dog towns located close to areas of human activity. Other than a few general statements and a hand-drawn map of the area, this plague epizootic was not well documented. The duration and extent of the epizootic and the effectiveness of the treatment are unknown.

The next recorded plague event started in November 1988 in the northeast corner of the Refuge. Mapping of prairie dog towns on the Refuge had just been completed (October 1988) in response to the discovery of a communal bald eagle winter roost in 1986. Due to the importance of prairie dogs as a food source for wintering bald eagles, increased attention was given to controlling this epizootic. Plague rapidly spread through a large (>600 ha) prairie dog town on the eastern portion of the Refuge and reached the southeast corner of the refuge in 20 days (J. Harrison, oral commun., 1994).

Previous studies have indicated that permethrin dust was effective at reducing fleas in burrows and on prairie dogs (Beard and others 1992; Barnes, 1993). A large quantity of permethrin powder was obtained and applied in prairie dog burrows in attempts to control plague, mostly in the interest of public health. The plague epizootic continued through September 1989, reducing prairie dog towns on the Refuge by 95 percent. Although the effects of plague on prairie dog towns was well documented during this event, the techniques involved with application of permethrin powder were not. It is believed that application rates were as suggested on the product label (1–2 oz/burrow) and that pressurized applicators were used. It is unknown, however, when and where (before, during, or after the passage of plague, or in active or inactive towns) the powder was applied. This lack of information hindered development of strategies to control future epizootics.

A prairie dog relocation program began in August 1989 (table 1). A standardized approach to prairie dog relocation techniques was developed in order to maximize efficiency and success of the relocation efforts. The FWS developed cooperative agreements with several private relocator groups from the Denver area. These groups were composed of private citizens who advocated saving prairie dog towns from destruction caused by the rapid growth of urban development. Prairie dogs were collected for relocation by a number of methods, including water flushing, vacuum truck, and live trapping.

Following the large-scale and successful relocation program (tables 1 and 2; 6,842 prairie dogs relocated through 1993, yielding >980 ha of active prairie dog towns in 1994), plague once again hit in May 1994, starting in the northeastern portion of the Refuge. The progression of this epizootic followed the same path as the one in 1988–89, proceeding south and east through a large (>400 ha) town on the east side of the Refuge. Several attempts were made to halt the advance of plague by dusting with permethrin powder on active portions of prairie dog towns in advance of the epizootic. Visual observation of prairie dogs above ground was used to determine where to begin dusting and to map the extent of plague. Plague continued to advance (much as wildfire spreads), slowing in its progress for several days to a few

Table 1. Summary of black-tailed prairie dog (*Cynomys ludovicianus*) relocations at Rocky Mountain Arsenal National Wildlife Refuge from 1989 to 2002.

	Source		
Year	**On refuge**	**Off refuge**	**Total**
1989	132	579	711
1990	447	2,525	2,972
1991	252	2,125	2,377
1992	229	438	667
1993	48	67	115
1994	175	0	175
1995	276	140	416
1996	43	1,711	1,754
1997	207	1,659	1,866
1998	269	502	771
1999	90	0	90
2000	208	0	208
2001	261	0	261
2002	309	0	309
Total	2,946	9,746	12,692

weeks as it encountered dusted areas, but eventually continuing to spread to all areas of the prairie dog town. By the fall of 1994, plague had decimated approximately 695 ha (or about 70 percent of the area occupied in May 1994) and had moved to the western portion of the Refuge. Plague continued throughout the winter. By the following spring, only about 73 ha of active prairie dog towns remained, and by September 1995, only 9 ha of active prairie dog towns remained (table 2). The second large-scale relocation program began shortly thereafter, and by the time this effort was winding down in 1998, over 4,000 prairie dogs had been relocated onto the Refuge from outside sources. The population rebounded quickly, reaching over 350 ha of active prairie dog towns after relocation of 5,072 prairie dogs (table 1), and continuing to grow to over 660 ha by 2000 (table 2), when the next epizootic arrived.

In January 2000, inspection of a prairie dog town at the northeast corner of the Refuge revealed no living prairie dogs. A plague control program was instituted immediately, with crews applying 35.9 kg of permethrin powder on about 40 ha of prairie dog towns within 1.6 km of the plague site by February 2, 2000. No other plague activity was observed on the Refuge until April 18, 2000, when a contractor working on a nearby remediation project found a dead prairie dog approximately 1.6 km from the earlier outbreak of plague. The carcass was sent to the Centers for Disease Control (CDC), and plague was confirmed on April 19, 2000. The plague control program was started again on April 20, 2000, concentrating on towns within 1.6 km of where the carcass had been found. Additional dead prairie dogs were found during May 2000 (plague positive), and the scope of plague control was expanded. By the end of June 2000 all active prairie dog towns in adjoining sections (about 51 ha) were dusted.

During the course of this epizootic, a product evaluation study on Deltadust® (Aventis Environmental Health, Montvale, N.J.) began. Deltadust (a powdered formulation of deltamethrin) is a relatively new product containing a synthetic pyrethroid similar to permethrin and is reportedly waterproof, providing insecticidal action for up to 8 months. From July to October 2000, the FWS, assisted by plague lab personnel from the CDC in Fort Collins, Colo., evaluated Deltadust at the Refuge. The results of the study (Seery and others, 2003) indicated Deltadust was effective at reducing flea populations within prairie dog burrows and had a residual effect over 84 days posttreatment. No toxic effects were noted in the prairie dog population from application of Deltadust into the burrows. After initial results were obtained from this study, additional quantities of deltamethrin were obtained and used immediately in attempts to control the continued spread of the epizootic. From July to October 2000, approximately 46 ha of high priority prairie dog towns (important to wintering bald eagles, public use areas, burrowing owl breeding areas, etc.) were treated with deltamethrin. All of these sites were monitored over the winter (2000–01). The treated sites survived without any sign of plague whereas most of the areas dusted with permethrin had succumbed to plague. However, plague activity was observed again in the spring of 2001 (based on plague-positive carcasses) in limited, widely dispersed areas across the Refuge. Populations of prairie dogs on several, but not all, of the towns dusted with deltamethrin in the summer and fall of 2000 were eventually decimated from plague during 2001, 6 to 10 months after towns were treated.

Discussion of Plague Management

From 1988 to 2001, a variety of insecticides (carbaryl, permethrin, and deltamethrin) were used at the Refuge in attempts to control plague in prairie dogs. Early attempts were aimed mostly at providing protection in areas heavily used by humans and were generally ineffective at controlling plague in prairie dogs. By 1994, more emphasis was given to providing protection to the prairie dogs themselves and even attempting to stop the spread of plague. In some cases, when applied early, these actions were successful in halting the spread of plague. On the Refuge, studies also indicated significant flea reductions after burrows were dusted with permethrin, although flea numbers on prairie dogs returned to previous levels 10 to 18 days posttreatment (Karhu and Anderson,

Table 2. Black-tailed prairie dog (*Cynomys ludovicianus*) population estimates at Rocky Mountain Arsenal National Wildlife Refuge, 1988–2002. Three major plague epizootics occurred in prairie dogs on the Refuge: 1988–89, 1994–95, and 2000–02.

Year	Prairie dogs/ha (mean ± SE)	*n* (plots)	Area occupied (ha)	Estimated population	r[a]
1988[b]	20.2 ± 1.6	24	1,850.8	37,406	----
1989[b]	20.2[c]	---	99.8	2,017	-2.92
1990[b]	12.2 ± 2.0	6	232.9	2,842	0.343
1991	14.6 ± 1.08	10	555.56	8,134	1.05
1992	17.8 ± 1.79	12	663.27	11,793	0.371
1993	22.57 ± 1.77	12	737.05	16,636	0.344
1994	23.47 ± 1.31	10	982.75	23,065	0.327
1995 (May)	50.86 ± 9.49	9	72.86	3,708	-1.83
1995 (Sept.)	50.86 ± 9.49	9	9.0	458	-2.09
1996	41.16 ± 5.6	8	35.9	1,478	1.17
1997	54.8 ± 10.8	6	139.77	7,640	1.64
1998	32.8 ± 3.78	10	357.77	11,735	0.429
1999	24.5 ± 4.41	10	533.74	13,076	0.108
2000	----	----	666.75	----	----
2001 (May)	----	----	250.43	----	----
2001 (Oct.)	----	----	105.0	----	----
2002	28.4 ± 4.31	15	127.02	3,607	----

[a] r = per capita growth rate, ln[N(t+1)/N(t)].

[b] 1988–90 data from Stollar and Associates (1992).

[c] No data available, density estimated.

2000). At the “ball field” prairie dog town, for example, the application of permethrin dust in a timely manner saved a prairie dog town used for environmental education programs. This town, located west of the administration complex on the Refuge, was a popular stop for school groups on tours of the Refuge. On July 8, 1995, Refuge personnel found a dead prairie dog at the site. The carcass was sent to the CDC in Fort Collins, Colo., for testing. After receiving confirmation of plague, the entire prairie dog town was dusted (0.68 ha) with permethrin on July 12, 1995. No other prairie dog carcasses were found during that time. That town was used during visual counts (June) to estimate abundance, so the population was known (*n* = 77). Over the course of the next month, periodic visual counts were made to monitor effectiveness of the treatment. After a month the population stabilized at about 25 prairie dogs, a loss of about two-thirds of the population. There were no other signs of mortality from plague at the site over the next several years, and the population began a gradual rebound, growing to cover 7.3 ha by 2001.

It appears that Deltadust, when applied in the manner described by Seery and others (2003), significantly reduces flea populations within prairie dog burrow systems and on prairie dogs. Deltamethrin has a significant residual effect, with flea populations still at nondetectable levels by day 84. Cessation of mortality of prairie dogs following application of deltamethrin accompanied flea reductions caused by the treatment. By comparison, previous studies evaluating permethrin dust have reported low numbers of fleas after 84 days (Beard and others, 1992).

Deltamethrin represents an effective alternative to permethrin dust for controlling flea populations in prairie dog towns. Its relative effectiveness, ease of application, and safety should make it an important tool for managing plague epizootics in these animals. The long residual activity of deltamethrin suggests that single applications may reduce fleas throughout most of the season of plague activity, which typically occurs during the warmest 4 to 5 months of the year. These advantages also suggest that deltamethrin can be useful for protecting prairie dogs as an important habitat component for raptors and other carnivores, such as black-footed ferrets, at wildlife conservation locations (for wintering, breeding, and translocation).

References Cited

Barnes, A.M., 1993, A review of plague and its relevance to prairie dog populations and the black-footed ferret, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 28–37.

Beard, M.L., Rose, S.T., Barnes, A., and Montenieri, J., 1992, Control of *Oropsylla hirsuta*, a plague vector, by treatment of prairie dog burrows with 0.5% permethrin dust: Journal of Medical Entomology, v. 29, p. 25–29.

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Ebasco Services, Inc., 1989, Black-tailed prairie dog—activity survey interim report: Prepared for the U.S. Army Program Manager’s Office for the Rocky Mountain Arsenal Contamination Cleanup.

Fagerstone, K.A., 1983, An evaluation of visual counts for censusing ground squirrels, *in* Kaukeinen, D.E., ed., Vertebrate pest control and management materials, fourth symposium: Philadelphia, Pa., American Society for Testing and Materials, ASTM ATP 817, p. 239–246.

Fagerstone, K.A., and Biggins, D.E., 1986, Comparison of capture-recapture and visual count indices of prairie dog densities in black-footed ferret habitat: Great Basin Naturalist, v. 8, p. 94–98.

Karhu, R.R., and Anderson, S., 2000, Effects of pyriproxyfen spray, powder, and oral bait treatments on the relative abundance of fleas (Siphonaptera: Ceratophyllidae) in black-tailed prairie dog (Rodentia: Sciuridae) towns: Journal of Medical Entomology, v. 37, p. 864–871.

Menkins, G.E., Biggins, D., and Anderson, S., 1990, Visual counts as an index of white-tailed prairie dog density: Wildlife Society Bulletin, v. 18, p. 290–296.

Seery, D.B., Biggins, D.E., Montenieri, J.A., Enscore, R.E., Tanda, D.T., and Gage, K.L., 2003, Treatment of black-tailed prairie dog burrows with deltamethrin to control fleas (Insecta: Siphonaptera) and plague: Journal of Medical Entomology, v. 40, p. 718–722.

Stollar and Associates, 1992, Biota annual monitoring report for 1990 and summary report for 1988 to 1990, comprehensive monitoring program, final report: Prepared for Rocky Mountain Arsenal Field Office, U.S. Fish and Wildlife Service, 16 p.

U.S. Fish and Wildlife Service, 1990, Annual Progress Report: Commerce City, Colo., Rocky Mountain Arsenal Field Office, 177 p.

U.S. Fish and Wildlife Service, 1994, Annual Progress Report: Commerce City, Colo., Rocky Mountain Arsenal Field Office, 182 p.

Vaccination as a Potential Means To Prevent Plague in Black-footed Ferrets

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Abstract

This study was conducted to further assess the feasibility of vaccinating black-footed ferrets (*Mustela nigripes*) against plague (caused by the bacterium *Yersinia pestis*). On days 0 and 28, 17 postreproductive ferrets were immunized by subcutaneous injection with a recombinant fusion protein containing F1 and V antigens from *Y. pestis*. Another 17 animals received a placebo by the same route. Two weeks after the second immunization, mean antibody titers to *Y. pestis* F1 and V antigens were measured and found to be significantly higher in vaccinates than their preimmunization values ($P < 0.0001$) and significantly higher than the control values ($P < 0.0001$). Six months postimmunization, 16 vaccinates and eight controls were challenged with approximately 8,000 colony forming units of virulent plague by subcutaneous inoculation. Eleven of 16 vaccinates (69 percent) survived with no ill effects whereas all eight control animals died within 3–6 days. Two months later, the 11 surviving vaccinates were challenged again by ingestion of a plague-infected mouse. None of the animals showed any ill effects and all survived. In contrast, seven control ferrets fed infected mice died within 2–4 days, including one animal that did not actually ingest the mouse but was likely exposed to it. This study demonstrates that immunization of ferrets with the recombinant F1-V fusion protein can induce significant antibody responses and reduce their susceptibility to plague infection.

Keywords: black-footed ferrets, immunization, *Mustela nigripes*, sylvatic plague, vaccine, *Yersinia pestis*

Introduction

Sylvatic plague, caused by the bacterium *Yersinia pestis*, is primarily a disease of wild rodents that is transmitted between mammals via flea (Insecta: Siphonaptera) bite, direct contact, ingestion, or inhalation. Since its introduction into the United States in the early 1900s, plague has become firmly established in native rodent populations throughout the West, causing frequent epizootics (Barnes, 1993). For many species of wildlife, plague mortality has become a serious conservation issue. Over half of the North American rodent species of conservation concern (Hafner and others, 1998), including several species of prairie dogs (*Cynomys* spp.), reside within the range of plague in western North America (Barnes, 1982). In addition, the endangered black-footed ferret (*Mustela nigripes*), which relies almost exclusively on prairie dogs for food and shelter, is highly susceptible to plague and suffers high mortality upon infection (Williams and others, 1994; Rocke and others, 2004).

Current methods to control plague in prairie dog colonies include dusting burrows with insecticides after the onset of an epizootic and population reduction. Although these methods have limited success in controlling outbreaks in rodents, they may be applied too late to be effective for ferrets, and population reduction is inappropriate for an endangered species. Recent studies have shown that multiple doses of a recombinant vaccine, consisting of two fused plague antigens, F1 and V (F1-V protein), protect laboratory mice against the bubonic or pneumonic form of plague (Heath and others, 1998). In a pilot study conducted at the U.S. Geological Survey's National Wildlife Health Center (NWHC) in Madison, Wis., six of seven ferrets that received a three-dose regimen of F1-V protein via subcutaneous injection survived challenge with 7,800 colony forming units (CFU) of *Y. pestis* 3 weeks after their last booster dose (Rocke and others, 2004). The objectives of the study described herein were to assess vaccine efficacy with a larger group of animals and with a longer duration between vaccination and challenge (6 months).

Methods

Thirty-four ferrets (23 females and 11 males) were selected for this study at the U.S. Fish and Wildlife Service,

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National Black-footed Ferret Conservation Center (NBFFCC), Wheatland, Wyo. (now located near Wellington, Colo.), where the initial immunization and collection of baseline blood samples took place. All animals were 3–4 years of age and had been vaccinated previously against rabies and canine distemper. At the NBFFCC, animals were marked individually with subcutaneous embedded microchips (AVID® Microchip I.D. Systems, Folsom, La.) and housed individually in 2.5-cm wire-mesh cages (61 x 61 cm) with vinyl floors. Wooden nest boxes (45 x 22 x 28 cm) were attached to the exterior of the cages via 30-cm corrugated drain pipe. Bedding consisted of absorbent cellulose (ALPHA-dri™; Shepherd Specialty Papers, Watertown, Tenn.). The animals were fed 60–70 g of a raw horsemeat diet (Toronto Zoo Small Carnivore Diet; Milliken Meat Products, Ltd., Scarborough, Ontario, Canada) once daily. Water was provided ad libitum in ceramic bowls or sipper bottles.

For challenge experiments, all ferrets were transported to the NWHC where they were placed in a Biosafety Level 3 animal holding facility. Upon arrival, the animals were treated prophylactically for coccidiosis and housed individually in stainless steel cages as described previously (Rocke and others, 2004). The animals were fed Toronto Zoo Small Carnivore Diet or Dallas Crown Carnivore Diet (Dallas Crown, Inc., Kaufman, Tex.) when the Toronto Zoo Small Carnivore Diet was unavailable. Methods of anesthesia and blood sampling were described in Rocke and others (2004).

This study was reviewed and approved by NWHC's Animal Care and Use Committee and Biosafety Committee. All personnel handling plague-infected animals or carcasses were required to wear powered, air-purifying (Hepa-filtered) respirators with fullface shields, rubber aprons and boots, and double surgical gloves. In addition, personnel collecting and handling animals and conducting necropsies were required to take prophylactic antibiotics (as prescribed by occupational health physicians).

On days 0 and 28, 17 ferrets at NBFFCC received 0.5 mL F1-V vaccine-adjuvant preparation (100 µg of antigen) by subcutaneous injection between the scapulae. The F1-V fusion protein and our methods of preparing the vaccine have been described previously (Heath and others, 1998; Rocke and others, 2004). Seventeen control animals received a placebo of 0.5 mL of Dulbecco's Medium (Sigma Chemical Co., St. Louis, Mo.). One control animal was euthanized due to disease unrelated to vaccination; the rest were transported to NWHC the 12th week postvaccination where they were held in isolation for several months prior to plague challenge. During this period, two other animals (one vaccinate and one control) were euthanized due to disease issues unrelated to vaccination. The control animal had severe abscessation and edema of the neck region from which *Streptococcus zooepidemicus* was isolated. The vaccinate experienced acute, medically nonresponsive hind limb paresis. Upon histological examination, both animals were found to have kidney lesions (tubular nephrosis and glomerulopathy).

Six months postvaccination (day 178), six vaccinates and eight controls were challenged with 7,800 CFU of our *Y. pestis* challenge stock (CO92) described previously (Rocke and others, 2004); the bacteria were administered in 0.2 mL sterile saline by subcutaneous injection in the scapular region. Blood samples were taken from animals prior to first vaccination and on days 28, 42, and 167. Animals were monitored daily for signs of illness, and day of death was noted; severely debilitated animals were euthanized by CO_2 asphyxiation.

To determine if survivors were protected from further plague infection, the 11 vaccinated ferrets surviving 2 months after the initial subcutaneous challenge were bled to determine titers to plague antigens, and each was then orally challenged with a single plague-infected mouse; seven unvaccinated ferrets each fed a single infected mouse served as controls. For the oral challenge, 6-week-old mice were inoculated with a 0.1-mL volume of >4,000 CFU *Y. pestis* by intradermal injection. Upon death within 3 days after challenge, the mice were placed in the cage of each ferret. Any carcasses or parts of carcasses not ingested by ferrets within 3–4 hours were removed and discarded. Any ferrets surviving the second challenge were bled to determine antibody titers after 4 weeks and then euthanized by intracardiac injection of euthanasia solution (Euthasol; Delmarva Laboratories, Midlothian, Va.). In both experiments, dead or euthanized ferrets were immediately necropsied. Selected tissues were collected for bacterial isolation (Rocke and others, 2004) and histology.

Serology

Blood samples were collected in sterile glass serum separator tubes from all animals prior to immunization, boost, and challenge. Survivors were also bled after challenge. After centrifugation of blood samples, the serum was transferred to 2-mL polypropylene tubes and frozen at -20ºC for future analyses. Antibodies against F1 and V antigens were measured by using an enzyme-linked immunosorbent assay (ELISA) as previously described (Rocke and others, 2004).

Statistical Analysis

Antibody titers were transformed by calculating the $\log_{10}$ of the reciprocal titer value. Change in titer was then calculated by subtracting an individual animal's transformed preinoculation anti-F1 or anti-V titer from the transformed titer of each of that same animal's subsequent blood samples. Statistical difference in change of titer between groups was tested separately at each blood sampling period by using a one-tailed Mann-Whitney test at $P = 0.05$ (Zar, 1999). Difference in survivorship between groups was tested at $P = 0.05$ by using the Fisher Exact test (Zar, 1999), and days to death were compared by using a one-tailed Mann-Whitney test at $P = 0.10$.

Results

All 17 F1-V vaccinated ferrets developed significant antibody titers to both F1 and V antigens after immunization. In contrast, antibody titers of control animals remained negative. Geometric mean titers in anti-F1 and anti-V antibody increased significantly after the initial dose of vaccine was administered ($P < 0.0001$) and increased to even higher levels (means of 1:25,000 and 1:40,000, respectively) after the second dose, or boost ($P < 0.0001$) (fig. 1). Within 6 months, the mean anti-F1 and anti-V titers of vaccinates declined significantly ($P = 0.0004$ and $P < 0.0001$, respectively), although they were still significantly higher than their prevaccination titers ($P < 0.0001$) and the unvaccinated controls prior to challenge ($P < 0.0001$).

Eleven of the 16 vaccinated ferrets that were inoculated with *Y. pestis* survived the subcutaneous challenge and showed no signs of illness. The other five vaccinates became sick and died with an average time to death of 9.4 days. The first vaccinate died on day 4 with unusual gross lesions, including bloody diarrhea, multifocal hemorrhage throughout the intestines, and swollen kidneys. *Yersinia pestis* was isolated in low numbers from the spleen, and *S. zooepidemicus* was also isolated from the retropharyngeal lymph node. The three vaccinates that died on days 7 and 9 had gross lesions more consistent with unvaccinated controls (enlarged and slightly hemorrhagic lymph nodes, enlarged spleen, mottled lungs), and *Y. pestis* was isolated from numerous tissues from all three carcasses. The last vaccinate died on day 18 postchallenge. No *Y. pestis* was isolated from any tissue, but *S. zooepidemicus* was found in the spleen, lymph nodes, liver, lungs, heart, esophagus, and an abscessed region on the neck. In comparison, all eight unvaccinated controls inoculated with *Y. pestis* died within 3–6 days of challenge, with an average time to death of 4.3 days. All had gross lesions consistent with plague infection, and large numbers of *Y. pestis* were isolated from the tissues of all animals. Including the animals that had *S. zooepidemicus*, the survival rate of vaccinates was significantly higher than that of controls ($P = 0.02$), and time to death was significantly longer ($P = 0.02$). At the time of subcutaneous challenge, the mean anti-F1 titer of vaccinates that survived (9,030) was not significantly higher ($P = 0.165$) than that of vaccinates that died (5,580). The mean anti-V titer was significantly higher ($P = 0.035$), however, in surviving vaccinates (16,950) compared to those that died (9,030).

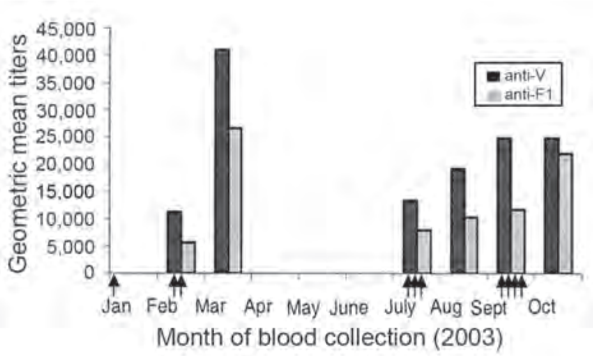

Figure 1. Geometric mean anti-F1 and anti-V antibody titers in black-footed ferrets (*Mustela nigripes*) immunized with F1-V protein. The dates of the first and second vaccinations (prime and boost), first subcutaneous challenge with *Yersinia pestis*, and second challenge via ingestion of infected mice are indicated with 1 arrow, 2 arrows, 3 arrows, and 4 arrows, respectively.

Two months after the subcutaneous challenge, the 11 surviving vaccinates received a second plague challenge via consumption of a plague-infected mouse. Each of them consumed an entire infected mouse, and all survived with no apparent clinical signs. In contrast, the seven control animals presented with infected mice all died within 2–4 days, including one animal that did not ingest its mouse but presumably licked or sniffed it; this animal died on day 4. *Yersinia pestis* was isolated from most of the controls, with the exception of one that died on day 2 that had an overwhelming infection of *S. zooepidemicus*.

Discussion

In this study, the majority (69 percent) of vaccinated ferrets survived subcutaneous plague challenge 6 months post-immunization in contrast to the unvaccinated controls that all died of the infection. These results are similar to those of our previous pilot study in which six of seven (86 percent) vaccinated ferrets survived subcutaneous challenge with the same dose of *Y. pestis* (Rocke and others, 2004). In that study, however, ferrets received an extra boost of F1-V just 3 weeks prior to challenge in a three-dose regimen whereas in the present study, the animals received only two doses and were not challenged with the bacteria until 6 months later. Mean anti-F1 and anti-V antibody titers of immunized animals increased significantly after vaccination, particularly after the boost; however, they decreased over the next several months to nearly preboost titers. Vaccinates that survived subcutaneous challenge had a slightly higher mean anti-V titer than those vaccinates that succumbed to the same challenge.

In nature, ferrets are likely exposed to plague by several means. They may be bitten by infected fleas as they navigate through burrows or as they feed on prairie dogs. It is also highly likely that ferrets contract plague while feeding on infected prairie dogs through either direct contact or inhalation of the bacteria. The one unvaccinated ferret in our study that contracted plague and died within 4 days even though it declined to consume the infected mouse is evidence of their extreme susceptibility to the bacteria via this route. Interestingly, in this study vaccinated ferrets that survived an initial subcutaneous challenge with *Y. pestis* all survived ingestion of an infected mouse 2 months later. This result suggests that flea-bite exposure of vaccinated ferrets in nature could potentially boost their immune response enough to ward off further plague infection via consumption of infected prey. We suspect that some vaccinated ferrets would also survive an initial oral challenge with infected mice. In a previous pilot study, two of five vaccinated ferrets survived after ingestion of infected mice as an initial challenge (T. Rocke, unpub. data, 2001). These results are promising but insufficient, so we are currently exploring methods for boosting mucosal immunity in vaccinates.

At least four ferrets in this study were found to have *S. zooepidemicus* infections, one prior to challenge and three after challenge. In addition, three other ferrets had kidney lesions (glomerulonephritis) visible upon histologic examination of tissues that may have resulted from a previous infection (T. Rocke, unpub. data, 2003). Kidney damage is a reported sequela to *S. zooepidemicus* infection in humans (Barnham and others, 1983; Francis and others, 1993; Pinto and others, 2001) and horses (Divers and others, 1992). Raw horsemeat has been a documented source of *S. zooepidemicus* for other small carnivorous mammals, including short-nosed bandicoots (*Isoodon macrourus*) and shrews (*Tupaia glis* and *Elephantulus rufescens*) (Shaw and others, 1984) and several primate species (Schiller and others, 1989). In our study, ferrets were fed raw horsemeat diets from two different sources, both at NBFFCC and NWHC. Samples of the meat were cultured after the infection was diagnosed, but the bacterium was not isolated. Even though the source of infection is still unknown, we believe many of our study animals may have had underlying *S. zooepidemicus* infections or were recovering from an infection. This bacterium may have significantly impacted the ability of vaccinated ferrets to withstand challenge to *Y. pestis*.

Summary

The results of this study suggest that two doses of the F1-V protein are sufficient to reduce ferret mortality from subcutaneous injection of plague for at least 6 months postimmunization, even in the face of a chronic, underlying *Streptococcus* infection. We suspect that vaccination of younger animals (<1 year old) and animals that are less stressed would result in even higher antibody titers, better resistance to the disease, and longer duration of immunity. Until other methods of plague control are developed, the F1-V vaccine could protect ferrets in captive breeding facilities and animals intended for release programs. Black-footed ferret kits and dams in captive breeding programs are fed wild prairie dogs that are captured, quarantined, and killed for that purpose. However, the loss of numerous captive ferrets at one facility from ingestion of plague-infected prairie dog meat demonstrated the potential hazard of this practice (Castle and others, 2001) even with disease precautions and quarantine of the prairie dogs. Vaccination of captive ferrets against plague could reduce this risk. Ferrets intended for release into the wild could be immunized with F1-V antigen several times prior to release and reimmunized upon recapture, preferably within 6 months to 1 year postrelease. This might reduce mortality rates of ferrets during plague outbreaks. However, because black-footed ferrets are completely dependent on prairie dogs for their survival and prairie dogs are likewise highly susceptible to plague, the ultimate recovery of ferrets will require maintenance of stable prey populations and thus prevention of plague in prairie dogs.

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References Cited

Barnes, A.M., 1982, Surveillance and control of bubonic plague in the United States: Symposia of the Zoological Society of London, v. 50, p. 237–270.

Barnes, A.M., 1993, A review of plague and its relevance to prairie dog populations and the black-footed ferret, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 28–37.

Barnham, M., Thornton, T.J., and Lange, K., 1983, Nephritis caused by *Streptococcus zooepidemicus* (Lancefield Group C): Lancet, v. 1, no. 8331, p. 945–948.

Castle, K.T., Biggins, D., Carter, L.G., Chu, M., Innes, M., and Wimsatt, J., 2001, Susceptibility of the Siberian polecat to subcutaneous and oral *Yersinia pestis* exposure: Journal of Wildlife Diseases, v. 37, p. 746–754.

Divers, T.J., Timoney, J.F., Lewis, R.M., and Smith, C.A., 1992, Equine glomerulonephritis and renal failure associated with complexes of group-C streptococcal antigen and IgG antibody: Veterinary Immunology and Immunopathology, v. 32, p. 93–102.

Francis, A.J., Nimmo, G.R., Efstratiou, A., Galanis, V., and Nuttall, N., 1993, Investigation of milk-borne *Streptococcus* *zooepidemicus* infection associated with glomerulonephritis in Australia: Journal of Infection, v. 27, p. 317–323.

Hafner, D.J., Yensen, E., and Kirkland, G.L., Jr., 1998, North American rodents—status survey and conservation action plan: Gland, Switzerland, International Union for the Conservation of Nature and Natural Resources/Species Survival Commission Rodent Specialist Group, 171 p.

Heath, D.G., Anderson, G.W., Jr., Mauro, J.M., Welkos, S.L., Andrews, G.P., Adamovicz, J.J., and Friedlander, A.M., 1998, Protection against experimental bubonic and pneumonic plague by a recombinant capsular F1-V antigen fusion protein: Vaccine, v. 16, p. 1131–1137.

Pinto, S.W.L., Sesso, R., Vasconcelos, E., Watanabe, Y.J., and Pansute, A.M., 2001, Follow-up of patients with epidemic poststreptococcal glomerulonephritis: American Journal of Kidney Diseases, v. 38, p. 249–255.

Rocke, T.E., Mencher, J., Smith, S.R., Friedlander, A.M., Andrews, G.P., and Baeten, L.A., 2004, Recombinant F1-V fusion protein protects black-footed ferrets (*Mustela nigripes*) against virulent *Yersinia pestis* infection: Journal of Zoo and Wildlife Medicine, v. 35, p. 142–146.

Schiller, C.A., Wolff, M.J., Munson, L., and Montali, R.J., 1989, *Streptococcus zooepidemicus* infections of possible horsemeat source in red-bellied tamarins and Goeldi’s monkeys: Journal of Zoo and Wildlife Medicine, v. 20, p. 322–327.

Shaw, M., Montali, R.J., and Bush, M., 1984, *Streptococcus zooepidemicus* in small carnivorous mammals fed uncooked horsemeat: Journal of Zoo Animal Medicine, v. 15, p. 161–164.

Williams, E.S., Mills, K., Kwiatkowski, D.R., Thorne, E.T., and Boerger-Fields, A., 1994, Plague in a black-footed ferret (*Mustela nigripes*): Journal of Wildlife Diseases, v. 30, p. 581–585.

Zar, J.H., 1999, Biostatistical analysis (4th ed.): Upper Saddle River, New Jersey, Prentice Hall, 929 p.

The Quest for a Safe and Effective Canine Distemper Virus Vaccine for Black-footed Ferrets

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Abstract

Canine distemper virus (CDV) causes a systemic disease that is highly virulent to mustelids and other carnivore (Order Carnivora) species and is found worldwide. Endemic canine distemper in wild and domestic carnivores in the United States has made reintroduction of endangered black-footed ferrets (*Mustela nigripes*) difficult in the absence of safe and effective CDV vaccines and vaccination practices. Toward this end, researchers have explored appropriate animal models and vaccine preparations in highly susceptible species. Published studies involving domestic ferrets (*M. putorius furo*) using Galaxy-D® and evaluating a recombinant canarypox-vectored vaccine for oral administration are reviewed. In addition, we present new findings in domestic and black-footed ferrets and Siberian polecats (*M. eversmannii*) that have extended our understanding of CDV in the black-footed ferret and other at-risk carnivore species. Original research presented here includes trials that determined an effective challenge dose (by route) of virulent CDV in domestic ferrets and Siberian polecats; the low likelihood of collateral vaccination with Galaxy-D; the adverse effect of modified-live virus boostering in black-footed ferrets receiving killed vaccine previously and the response of Siberian polecats receiving canarypox-vectored recombinant CDV vaccine (reCDV); the absence of an effect of reCDV vaccination on conception, pregnancy, and neonatal growth in Siberian polecats; and the apparent inefficacy of active reCDV vaccination during the period of passive immunity in young Siberian polecats. In the final section, we discuss emerging concerns and avenues for disease intervention that may present new opportunities to solve problems in vaccine safety, vaccine availability, field vaccine delivery, and other therapeutic modalities.

Keywords: black-footed ferret, canarypox, canine distemper, ferret, morbillivirus, oral vaccine, paramyxovirus, recombinant, Siberian polecat

Introduction

Canine distemper virus (CDV; family Paramyxoviridae, genus *Morbillivirus*) is a single-stranded, negative sense, 16-kilobase RNA virus encoding six genes (designated N, P, M, F, H, L) and eight protein products. The N gene has been used for diagnostic CDV identification (Wimsatt and others, 2001; Rzezutka and Mizak, 2002) while the M and P genes have been used in phylogenetic analyses (Barrett and others, 1993; Saliki and others, 2002) and subtype identification (Roelke-Parker and others, 1996; Carpenter and others, 1998; van de Bildt and others, 2002; Bronson and others, 2003), respectively. Phylogenetic analysis using other genes has repositioned CDV within the paramyxoviridae (Westover and Hughes, 2001). Vaccine developers have focused on hemagglutinin (HA) and fusion (F) gene product antigens, which appear to confer highly protective immunity when antibodies are successfully raised in response to vaccination.

Canine distemper virus is found worldwide. The hallmarks of CDV-induced disease are the result of primary host tissue tropisms for the cutaneous (maculopapular rash, erythema), respiratory (increased respiratory rate or labored respirations, dyspnea, cyanosis), gastrointestinal (diarrhea), and central and peripheral nervous systems. While respiratory and gastrointestinal manifestations of this disease can cause considerable morbidity and mortality, it is often the central nervous system manifestations that portend death during its clinical expression (Leisewitz and others, 2001). Nervous signs attributed to CDV include seizures, tremors, depression, and myoclonia (peripheral nervous signs). While some tissue tropism differences in CDV are expected, the Center for Veterinary Biologics (CVB; Veterinary Services, Animal and Plant Health Inspection Service, U.S. Department of Agriculture [USDA]) virulent challenge strain ultimately leads to neurological disease; nervous signs can also dominate in

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previously vaccinated mustelids that ultimately succumb to CDV infection (J. Wimsatt, unpub. data, 1996–98).

Canine distemper primarily affects carnivores (Order Carnivora), but may opportunistically infect other taxa (Appel and others, 1991; Svansson and others, 1993; Appel and Montali, 1994; Appel and Summers, 1995; Kennedy and others, 2000; Pollack, 2001; Noon and others, 2003). In terms of its risk to endangered carnivores, CDV is the most significant pathogenic virus known, and the black-footed ferret (*Mustela nigripes*) reintroduction program must address this ongoing threat to captive breeding and wild population stability (Williams and Thorne, 1996).

It is the general intent of this paper to accomplish two somewhat disparate goals. First, we chronicle what research on canine distemper virus prophylaxis in mustelids has revealed, the roles of various animal models and vaccine preparations in the quest, and where new discoveries could likely lead these pursuits in the future. Second, we present new findings of black-footed ferret responses to CDV vaccination and studies using CDV vaccines in surrogate animals to find a practical approach for CDV prophylaxis in susceptible *Mustela* species.

The Ecology of Canine Distemper Virus and the Risk It Presents to the Black-footed Ferret

Canine distemper virus is enzootic in urban and rural settings (Grinder and Krausman, 2001). Canine distemper virus becomes rapidly inactivated once in the environment (Fox and others, 1998) but is readily spread by aerosol, even under dry, hostile conditions (Williams and others, 1988, 1997). In the wild, transfer can occur at carnivore food (e.g., burrow entrances) and water sources. Wildlife epizootics may emerge as a consequence (Noon and others, 2003).

Traditionally, the primary reservoir and ultimate source of CDV outbreaks in the wild is assumed to be unvaccinated domestic dogs that infect wildlife with CDV during chance encounters. The potential role of wild carnivores (especially young) as primary reservoirs of CDV is difficult to discount (Guo and others, 1986; Gese and others, 1991, 1997; Williams and Thorne, 1996; Williams and others, 1997; Cypher and others, 1998; Grinder and Krausman, 2001; Arjo and others, 2003) since high CDV seroprevalence rates, suggestive of high levels of exposure, are found in several wild species (Guo and others, 1986; Gese and others, 1991, 1997; Williams and others, 1997; Cypher and others, 1998; Dunbar and others, 1998; Truyen and others, 1998; Grinder and Krausman, 2001; Ikeda and others, 2001). During a recent outbreak of CDV at an urban zoo, wild raccoons (*Procyon lotor*) were found to harbor a unique CDV variant (Lednicky and others, 2004), and they appeared to serve as a distinct reservoir. Most dogs are vaccinated for CDV (Greene and Appel, 1998); as a result, wild carnivores may be of greater infective potential to high-risk species, such as the black-footed ferret, than are domestic dogs. However, resident CDV in domestic dogs is under strong vaccine-induced selection pressure (Mochizuki and others, 1999; Hashimoto and others, 2001; Lednicky and others, 2004) and thus cannot be discounted as an emergent source in the future.

One area of growing relevance to captive and exotic carnivores is the possibility of CDV persistence and later viral shedding (elaboration and release of virus by renewed replication from the host at a later date) after the primary infection has subsided. This issue is of great concern where modified-live virus (MLV) vaccines are used in nontarget species.

Persistence of morbillivirus infections has led to such diseases as subsclerosing panencephalitis in humans (Dyken, 2001; Garg, 2002; Schneider-Schaulies and others, 2003), Paget’s disease (Cartwright and others, 1993; Fraser, 1997; Mee and others, 1998; Friedrichs and others, 2002; Hoyland and others, 2003), and canine orthopedic conditions (Mee and others, 1993; Harrus and others, 2002). Autoimmune-mediated demyelination associated with measles or CDV infection has been studied in relation to its possible association with multiple sclerosis (Anonymous, 1978; Appel and others, 1981; Cook and others, 1986; De Keyser and others, 2001; Hernan and others, 2001). A link between infectious obesity and CDV has been proposed as well (Dhurandhar, 2001; Verlaeten and others, 2001).

Recently, evidence of CDV persistence has been documented in domestic dogs in which selected strains of the virus survived without detection by the host immune system (Lincoln and others, 1971; Povey, 1986; Leisewitz and others, 2001). A major requirement for chronically persistent CDV infection involves the selection of a cell-associated strain with limited capability for antigen presentation (Vandevelde and Zurbriggen, 1995) and conferring only limited antibody diversity (Rima and others, 1987); this latter strain differs in its pathogenesis from more virulent forms causing acute disease (Vandevelde and others, 1980). One key site of CDV persistence may be dendritic cells, reflecting a change in CDV cell tropism (Wunschmann and others, 2000). The condition “old dog encephalitis” is one presentation of chronic CDV infection (Lincoln and others, 1971; Hall and others, 1979; Tobler and Imagawa, 1984; Evans and others, 1991; Axthelm and Krakowka, 1998). Moreover, a tropism for epithelial cells (in addition to the typical tropism for macrophages) in culture suggests that persistent strains behave more akin to vaccine strains (Evans and others, 1991). A recent case report highlighted the risk of CDV persistence from vaccine strains when a red panda (*Ailurus fulgens*) vaccinated 3 years earlier with a commercial MLV CDV vaccine developed progressive CDV-induced neurological disease and subsequently died (Bronson and others, 2003). Gene typing (P gene) demonstrated that the offending CDV isolate was actually the original vaccine strain. Another recent paper suggested that incomplete CDV expression of fusion (F) protein may facilitate persistent viral infection; likewise, hemagglutinin (HA) heterogeneity of new emerging strains could lead to more widespread CDV persistence if F protein immunity becomes the primary source of protection following vaccination (Meertens and others, 2003).

Animal Models for Testing CDV Vaccines Destined for the Black-footed Ferret

Historically, guidelines for vaccinating free-ranging and captive wild carnivores were derived from those used for vaccines in domestic dogs, mink (Hagen and others, 1970), and domestic ferrets (*M. putorius furo*) (Hagen and others, 1970; Farrell and others, 1971). Interestingly, while domestic dogs are commonly vaccinated, they are not among the most CDV-susceptible carnivore species. One study estimated that up to 70 percent of urban dogs that were exposed to natural CDV infection never developed overt disease signs although they seroconverted, suggesting occult infection (Rockborn, 1957). Likewise, experience has shown that vaccines developed for high efficacy in dogs (and also sometimes used safely in some wild canids) may be too virulent for more susceptible species (Fox and others, 1998) such as red pandas (Bush and others, 1976; Itakura and others, 1979; Montali and others, 1983; Appel and Summers, 1995), gray foxes (*Urocyon cinereoargenteus*) (Halbrooks and others, 1981), and selected *Mustela* species (Carpenter and others, 1976; Montali and others, 1983, 1994; Sutherland-Smith and others, 1997). Canine cell line origin passaged vaccines were quickly realized to be pathogenic to domestic ferrets, commonly vaccinated as pets against CDV (Fox and others, 1998). Early MLV CDV vaccines intended for ferrets utilized primary chick embryo passage. These procedures were expensive, and assuring product uniformity was an ongoing concern (Fox and others, 1998).

An immune deficiency in black-footed ferrets that may be of prime importance in explaining the unique, extreme susceptibility of this species to CDV and other infectious diseases is the diminished production of the proimmune cytokine interleukin-6 (Stoskopf-Kennedy and others, 1997). In contrast, Siberian polecats (*M. eversmannii*) appear to produce greater amounts of interleukin-6 (S. Wisely, oral commun., 2004). Homozygosity among Wyoming black-footed ferrets is recognized from genetic comparisons to historical populations from Kansas and to Siberian polecats (Wisely and others, 2002); this limited diversity may have contributed to the unique susceptibility of black-footed ferrets to natural and vaccine strains of CDV. Further investigations will reveal whether other highly susceptible species exhibit the same predisposition to diminished interleukin-6 production. Other cytokines need to be explored in this light as well (Bencsik and others, 1996; Grone and others, 2002).

A recent refinement in the production of one widely used CDV vaccine strain involved serial passage of the virus on an immortal primate Vero cell line (rather than chick embryo) and a more controlled process of vaccine attenuation. These procedures appear to improve product reliability, but highly susceptible species still succumb to vaccine-induced viral disease (Sutherland-Smith and others, 1997).

The characterization of appropriate models for the study of CDV vaccines in susceptible species has been a high priority. Based on taxonomy, domestic ferrets appeared to provide a close model for interpreting the likely CDV responses of black-footed ferrets as compared with other carnivores; more closely related Siberian polecats (O'Brien and others, 1989) and black-footed ferret × polecat hybrids helped to further define the likely impact and efficacy of existing vaccine strategies destined for the black-footed ferret (Williams and others, 1996). Recently, surplus black-footed ferrets have sometimes been available for CDV vaccine studies (J. Kreeger, oral commun., 2004), but definitive challenge studies may still rely heavily on other mustelid models.

Vaccines: the Past, Present, and Future

Traditionally, killed virus (KV) vaccines were reserved for species and situations where MLV vaccines were considered unsafe. Potential disadvantages of KV vaccines include: unreliable inactivation; short-lived immunity (in addition, adjuvants that may cause some side effects may be required); the need for high antigenic doses (possible side effects if redosed); variable protection in poor responders; and finally, the induction of humoral (antibody production) rather than cell-mediated (i.e., T cell-mediated cellular) immunity (Schultz and Zuba, 2003). Thus, KV vaccines may not protect against overwhelming exposures to wild-type CDV; protection in such instances likely requires both robust humoral and cell-mediated immune responses. A nonadjuvanted KV vaccine was produced for use in highly susceptible species such as the black-footed ferret and red panda by Dr. Max Appel, of the Baker Institute at Cornell University; this vaccine was provided until a more favorable vaccination strategy became available.

Commercial CDV vaccines are primarily modified-live products incorporating carefully selected wild strains that respond favorably to serial passage and graded attenuation. Of these, the Onderstepoort strain has been most extensively used for vaccination in the domestic ferret and exotic carnivores in zoological collections, first as the chick-embryo product Fromm-D (Solvay Co., Mendota Heights, Minn.; no longer produced) and later as the primate Vero cell line attenuated vaccine, Galaxy-D® (Schering-Plough Animal Health, Inc., Union, N.J.). As a rule, modified-live products do not supply sufficient antigenic load to confer immunity unless active infection is engendered by vaccination (Schultz and Zuba, 2003). A recent study on the efficacy of Galaxy-D in domestic ferrets demonstrated, by polymerase chain reaction (PCR) amplification, the presence of CDV vaccine virus in the blood

5 days following the first of two inoculations. A primary vaccination series led to protective immunity as defined by virulent strain challenge (Wimsatt and others, 2001). Modified-live CDV vaccines have been shown to provide substantial and long-lived immunity following a primary vaccination series that invokes both cell-mediated and humoral immunity in dogs and domestic ferrets (Gorham, 1966, 1999). In the past, Fervac-D® (United Vaccines, Inc., Madison, Wis.) and other modified-live CDV vaccines (Fromm-D and Galaxy-D) routinely used in domestic ferrets were tested in surrogate species and were found unsuitable for black-footed ferrets. Either primary (CDV-induced) or secondary immunosuppression-related disease ensued when black-footed ferrets and black-footed ferret hybrids were vaccinated with these formulations (E. Williams, oral commun., 1995). Lymphocyte apoptosis accompanies CDV infection leading to its immunosuppressive effects (Moro and others, 2003a,b). As with natural infection, the immunosuppressive fallout of CDV infection from modified-live vaccination can lead to significant secondary morbidity and mortality in stressed or particularly susceptible individuals. The closely related measles and CDV viruses directly inactivate lymphocytes by virus-dependent and independent means (Krakowka, 1982) whereas more “adapted” strains do not inhibit lymphocyte proliferation (Schultz, 1976; Schlender and others, 1996) or T cell-mediated cytotoxicity (Tipold and others, 1999), and lead to the elaboration of immune-modulatory substances (Krakowka and others, 1987; Tipold and others, 1999).

Our interest in modified-live CDV vaccination in the black-footed ferret arose in exploring the possibility that a reliable, less virulent, modified-live vaccine might be used to booster black-footed ferrets that had been vaccinated previously with a KV vaccine. A modified-live CDV booster would be expected to last for the reproductive life of the animal, thus obviating the need for vaccination in the wild after reintroduction. Experimental KV vaccine (inactivated Onderstepoort strain) was widely used by zoos to protect high-risk species such as lesser pandas and black-footed ferrets (R. Montali, oral commun., 1996), but a vaccinated cohort had never been extensively challenged under controlled conditions to determine efficacy because of the scarcity and inherent value of these species. Use of a CDV modified-live booster following repeated KV vaccination served as a mild challenge. Boostering efficacy was further tested by subsequent virulent strain challenge. Based on experience gleaned from studies on surrogate species and hybrids with various candidate vaccines, current vaccine trials now focus primarily on safer subunit vaccines for genetically “bottlenecked” or exquisitely susceptible species.

More recently, the advent of vectored vaccines employing a wide range of different vectors and supplying antigens for many diseases affecting many species (Tartaglia and others, 1990, 1992, 1993; Paoletti and others, 1993, 1994, 1995; Taylor and others, 1994; Pincus and others, 1995) has fostered new optimism about the potential to find a safe and effective CDV vaccine for use in highly susceptible species.

Recent Studies Guiding Use of CDV Vaccine in Mustelids

All animals undergoing vaccine and challenge trials described below were housed in a biosafety level-2 room in modified rabbit cages and fed a high quality cat (Siberian polecats or domestic ferrets) or mink (black-footed ferret) chow; water was provided free choice. Animals were randomly assigned to treatment groups unless otherwise specified and grouped in cage racks by treatment. All animals were supplied with 40.6-cm (10.2-cm diameter) PVC hide tubes with fixed end caps. Animals were anesthetized without restraint by placing a second end cap with an inhalant anesthetic delivery port over the opposite end while the animal was inside.

Anesthesia was induced using 5 percent isoflurane in 3 L/min oxygen. After approximately 2 minutes, the animal was transferred from the PVC chamber to a face mask, and anesthesia was maintained at 1–2 percent isoflurane in 1.5 L/min oxygen. Care was taken to anesthetize the controls before the vaccinates in all cases. Blood samples (1 mL) were collected from the cranial vena cava or from an external jugular vein into serum tubes, and serum was frozen until assayed. Under anesthesia, vaccination was accomplished by subcutaneous injection (Galaxy-D, following the manufacturer’s instructions, and canarypox-vectored recombinant canine distemper virus [reCDV] vaccine), or by the oral route (reCDV), spraying the reconstituted vaccine in the back of the mouth.

Serology and Challenge Strain Dose Validations

An adapted standard serum microneutralization test was used to assess CDV titers (Appel and Robson, 1973). All virulent CDV challenge studies employed the CVB USDA Snyder Hill virulent challenge strain (Lot # 90-18). This same strain is used for vaccine challenge studies required for USDA licensing of commercial CDV vaccines. Dose selection for these studies was validated as described below.

Initial challenge dose-response studies using six domestic ferrets per group and five dose groups (J. Wimsatt, unpub. data, 1996) established a minimal 100 percent lethal intraperitoneal dose of CVB Lot # 90-18 challenge strain ferret spleen suspension in domestic ferrets as a dilution of 1:1,000 (pH 7.0, delivered in 1 mL total volume). Thus, for all subsequent challenge studies, regardless of the *Mustela* species tested, a 1-mL volume of challenge strain diluted to 1:250 in phosphate buffered saline (same pH and total volume) was used. This final lethal dose selected for challenge studies was confirmed in four Siberian polecats (J. Wimsatt, unpub. data, 1996) and was also found to be 100 percent effective (lethal) when used in challenge controls in subsequent studies. Later investigations extended these initial determinations to suggest that combined oral/intranasal instillation yielded the same results as intraperitoneal administration in Siberian polecats (J. Wimsatt, unpub. data, 1997) and domestic ferrets (Wimsatt and others, 2001). The only exception was that CDV-induced skin erythema or maculopapular rash usually occurred first at the site of challenge strain inoculation.

Challenge studies still remain the best available means to test vaccine efficacy. The significance of different routes of challenge, like those influencing vaccination, may be of considerable importance and requires careful study (Schultz and Zuba, 2003). While intracerebral and intraperitoneal challenge are commonly used, mucosal (intranasal/oral) challenge more closely mimics natural infection. Mucosal immunity is often considered the first line of defense against infectious agents (Ogra and others, 1980). In our studies, using survival as the endpoint, the intraperitoneal and oral/intranasal routes yielded similar results. This is of interest since CDV has a tropism for mucosal tissue (Jozwik and Frymus, 2002), and mucosal presentation to dendritic cells may stimulate cell-toxic lymphocytes (Etchart and others, 2001) early in the disease pathogenesis. Likewise, active CDV mucosal immunization may minimize disease-induced immunosuppression (Liashenko and others, 1999) or bypass maternal passive immunity (Fischer and others, 2002), leading to qualitatively different outcomes during challenge and vaccination. During challenge, such differences were not evident.

Modified-live Vaccine Studies in Domestic Ferrets

A chick embryo origin product (Fromm-D) using an attenuated Onderstepoort strain was found to be safe and effective when tested in black-footed ferret × Siberian polecat hybrids (Williams and others, 1996) and domestic ferrets (Fox and others, 1998). Galaxy-D was tested in male domestic ferrets vaccinated and challenged as described previously (Wimsatt and others, 2001). Briefly, eight randomly selected CDV-seronegative male domestic ferrets (Marshall Farms, Rose, N.Y.) were subcutaneously vaccinated twice 4 weeks apart with Galaxy-D according to the manufacturer's instructions. Eight control animals received saline injections. Challenge followed 21 days after the last vaccination (Wimsatt and others, 2001).

Virulent virus challenge produced 100 percent mortality in the controls, with prolonged presence of virus nucleoprotein in the blood detected by CDV-specific nucleoprotein reverse transcriptase PCR (RT-PCR). All Galaxy-D vaccinates (*n* = 8) survived following a primary two vaccine series although one first-time and two second-time vaccinates expressed viral nucleoprotein in their blood following challenge (Wimsatt and others, 2001). After active infection, this MLV vaccine induced a robust immune response protective against lethal CDV challenge, indicating that domestic ferrets responded with protective adaptive immunity to this same CDV strain, originally packaged in the avian embryo passaged Fromm-D vaccine.

Domestic Ferret Collateral Vaccination of Cage Mates

In a second study, randomly selected pair-housed male CDV-seronegative domestic ferrets were subcutaneously vaccinated with a single dose of Galaxy-D. Blood sampling for serology and challenge were performed as indicated in fig. 1. Unvaccinated CDV-naïve cage mates were blood-sampled for seroconversion to assess for collateral vaccination.

None of the six male co-housed domestic ferrets seroconverted in response to a single Galaxy-D delivered to their (CDV-naïve) cage mate up to 25 days after vaccination. All vaccinated ferrets (six of six) survived challenge following the single Galaxy-D dose. Serology values for unvaccinated cage mates, vaccinates, and unvaccinated controls are shown in fig. 2; titers for unvaccinated cage mates housed contemporaneously with Galaxy-D vaccinates remained low and indistinguishable from those of seronegative controls (fig. 2), suggesting that if primary vaccine shedding or contamination following vaccination occurred, it was insufficient to produce a MLV-induced immune response in the CDV-naïve cage mates.

Subcutaneous vaccination of CDV-naïve domestic ferrets with Galaxy-D did not appear to present a sufficient antigenic dose for collateral vaccination of co-housed cage mates and thus did not lead to seroconversion. This is not surprising since modified-live virus load is typically too low to induce an immune response in the absence of a host infection (i.e., host infection replicates more virus, thus increasing its antigenic load) caused by the vaccine strain (Schultz and Zuba, 2003). However, the timeframe was not sufficient to conclude that shedding of the Galaxy-D CDV virus from vaccinates would not have occurred eventually from virus replication in the host.

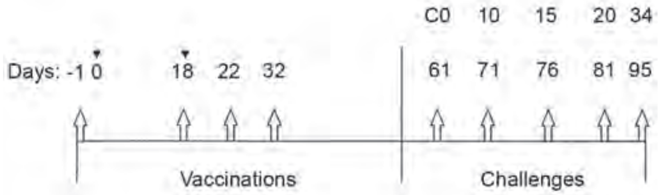


Figure 1. Timeline for the black-footed ferret (*Mustela nigripes*) Galaxy-D booster and virulent canine distemper virus challenge study. Seronegative domestic ferrets (*M. putorius furo*) in the same room served as challenge strain controls, and another cohort of pair-housed domestic ferrets had one member of the pair randomly selected for Galaxy-D vaccination at the same time; vaccinates were later challenged with the others while the unvaccinated member of the pair was removed just prior to challenge. Triangles indicate days of vaccination. Arrows indicate days when blood samples were drawn.

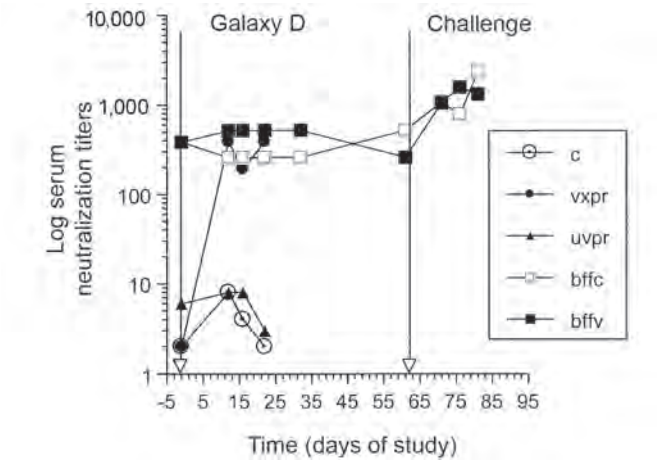


Figure 2. Serum neutralization titers for domestic ferret (*Mustela putorius furo*) controls (c), vaccinated domestic ferrets (vxpr), pair-housed unvaccinated domestic ferrets (uvpr), previously vaccinated older black-footed ferrets (*M. nigripes*) receiving Galaxy-D boostering prior to challenge (bffv), and previously vaccinated older black-footed ferrets challenged with canine distemper virus (bffc). Controls and unvaccinated pair-housed domestic ferrets did not exhibit significant titer increases. Black-footed ferrets started with high median titers from previous vaccinations, but boostering with Galaxy-D had no significant effect on their titers. Challenge caused elevated titers in the survivors.

Black-footed Ferrets

Nonreproductive, older (6–8 years), mixed-sex black-footed ferrets (culled from the breeding program) that had previously received one or more experimental KV vaccinations (an Onderstepoort strain-origin experimental vaccine produced by M. Appel, Baker Institute, Cornell University) were randomly assigned to one of two treatment groups after being matched for CDV serum neutralization titer across groups prior to study. At the beginning of the study, the first group (*n* = 8) received a single dose of Galaxy-D subcutaneously while the second group (*n* = 7) served as controls. Surviving vaccinates (*n* = 6) and controls (*n* = 5) were challenged 61 days later. The timeline for the experiment is shown in fig. 1. The primary endpoint of interest was survival although necropsies were performed to determine pathological changes following challenge as well as the cause of death.

Serum neutralization titers in surviving black-footed ferrets revaccinated with Galaxy-D and previously vaccinated (with the M. Appel killed CDV vaccine) black-footed ferret controls were comparable to those observed in newly vaccinated domestic ferrets receiving Galaxy-D for the first time. As expected, these titers contrasted sharply with those of unvaccinated seronegative domestic ferret controls (fig. 2). Prior to challenge, one black-footed ferret with a titer of 1:8 from prior vaccination succumbed (one of eight) to vaccine strain CDV 15 days after vaccination, and another died from a secondary infection, likely related to CDV-induced immunosuppression (*Clostridium* sp. was isolated from this case of vascular sepsis). In addition, a control black-footed ferret (unvaccinated during the present trial) succumbed to CDV (one of seven; it succumbed 32 days after vaccine delivery and had an initial titer of 1:64) although it was housed in a separate rack of cages adjacent to the black-footed ferret vaccinates. Following challenge, three of six vaccinates died, one 17 days after challenge (1:512). Of black-footed ferret controls, when they were finally challenged, one died 11 days later, and another died in response to a secondary infection (*Enterobacter faecalis*-induced sepsis). All black-footed ferret challenge survivors developed elevated CDV titers.

Previously, CDV-naïve black-footed ferrets were shown to be highly susceptible to the development of canine distemper even when the virus (canine passaged) was supplied by vaccination as a modified-live CDV strain (Carpenter and others, 1976). The presence of high titers from the KV vaccine appeared protective for black-footed ferrets exposed to live attenuated CDV in vaccine (Galaxy-D) or to the challenge strain; nevertheless, high titers alone were not always indicative of protection, as illustrated by one animal with a high titer (1:512) that still succumbed to CDV. From this series, MLV boostering of black-footed ferrets with high circulating CDV titers was of marginal value, most likely due to the blocking effect of these antibodies on the vaccine strain. There is no evidence that cell-mediated immunity was enhanced from boostering. Even so, overall, titers above 1:64 in this series appeared to confer protection against CDV challenge. Perhaps more important was the observation that protection against CDV did not necessarily ameliorate the likelihood of immunosuppression and death from secondary invaders. Finally, of those succumbing to CDV, the precipitous onset of neurological signs, without other prodromal signs, was the hallmark of disease development in prior vaccinates. This has been explained as a persistence of F protein-directed immunity with waning HA protection and is qualitatively similar to the outcome observed when CDV-infected vaccinates encounter novel CDV strains where HA antigenicity has shifted (Stern and others, 1995).

Canarypox-vectored Vaccination and the Potential for Oral Vaccine Delivery

A dose-response study was performed to define the minimum protective dose and chronicle possible side effects of an experimental canarypox-vectored recombinant CDV vaccine (reCDV) in Siberian polecats, as described in detail elsewhere (Wimsatt and others, 2003). Briefly, subcutaneous dose groups received $10^{5.5}$, $10^{5.0}$, or $10^{4.5}$ plaque-forming units (PFU, a measure of vector and therefore vaccine concentration), and oral dose groups received $10^{8.0}$ and $10^{5.5}$ PFU. The timeline used for vaccination, blood sampling, and challenge is shown in fig. 3; challenge was performed 61 days after the

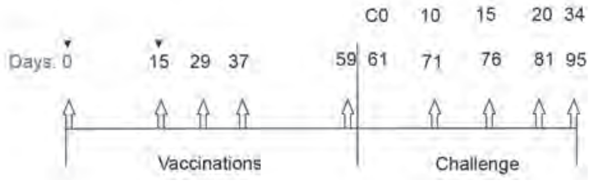


Figure 3. Timeline for canarypox-vectored recombinant canine distemper virus vaccine (reCDV) trials in Siberian polecats (*Mustela eversmannii*) and in the reCDV-Galaxy-D boostering study where the same timeline was used except that Galaxy-D was substituted for the second reCDV vaccination. Triangles indicate days of vaccination. Arrows indicate days when blood samples were drawn.

first vaccination. For standardization purposes, only vaccine expressing >95 percent expression-capable canarypox vaccine vector was used. Outcomes included CDV-associated clinical sign development, survival of virulent challenge postvaccination, and antibody development; only the latter two outcomes will be recounted here.

As previously reported, oral reCDV vaccination of Siberian polecats with $10^{8.0}$ PFU vaccine was protective for five of six vaccinates, or 83.3 percent effective in protecting Siberian polecats against lethal CDV challenge (Wimsatt and others, 2003). A difference in survival following challenge was noted in groups receiving the same vaccine dose ($10^{5.5}$ PFU) by different routes (oral vaccine, none of six survived challenge; subcutaneous vaccine, three of six survived) indicating that the parenteral route was superior to oral delivery. The difference in challenge survival between the $10^{5.5}$ PFU (three of six survived) and $10^{5.0}$ PFU (three of five survived) subcutaneous dose groups was not significant, suggesting the minimal protective CDV PFU dose is higher than $10^{5.5}$.

A Kaplan-Meier survival analysis was performed with dose and route of reCDV administration as predictors (fig. 4) (Wimsatt and others, 2003). Protective titers in response to reCDV were typically lower than those measured following vaccination with Galaxy-D in naïve animals; higher relative titers in response to reCDV were associated with greater protective value of the vaccine, and generally predictive of vaccine efficacy overall, as was the case for the modified-live vaccine. Even so, some challenge survivors that received reCDV had titers low enough that they would have been predicted to succumb to the challenge if modified-live vaccine protective titers were used as a guideline (e.g., 1:50–100; see fig. 5). It seems plausible that the protective titer differential between reCDV and modified-live vaccines in challenge survivors reveals that cell-mediated immunity conferred by the reCDV vaccine is a major aspect of its protective effect.

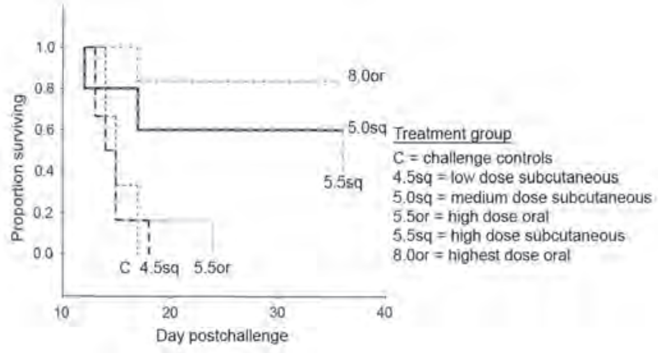


Figure 4. A survival curve is shown for canarypox-vectored recombinant canine distemper virus vaccine trials with Siberian polecats (*Mustela eversmannii*). Animals receiving two $10^{8.0}$ PFU vaccinations orally (8.0or) survived. Those receiving lower subcutaneous doses (e.g., 5.0sq) had lower survival as did those receiving lower oral doses (e.g., 5.5or), which fared even worse. (From Wimsatt and others, 2003. Reprinted with permission of the *Journal of Zoo and Wildlife Medicine*.)

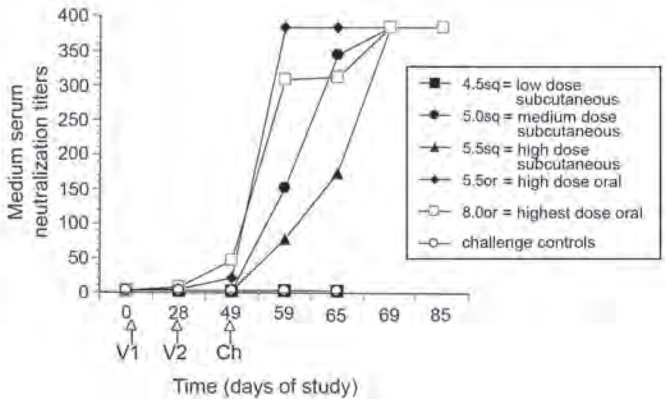


Figure 5. Serology results from the canarypox-vectored recombinant canine distemper virus (CDV) vaccine dose-response study where varied doses were administered subcutaneously or orally under isoflurane anesthesia. These results indicated that survivors mounted CDV serum neutralization titers above those of nonsurvivors. An exception was noted in the case of the oral $10^{5.5}$ group, where nonsurvivors mounted elevated titers, but these titers were insufficient for protection against challenge. Thus, a cell-mediated component of immunity, mounted at higher protective vaccine doses, must be important for vaccine efficacy with vectored subunit vaccines against CDV. V1 = first vaccination, V2 = second vaccination, Ch = challenge. (Adapted from Wimsatt and others, 2003. Reprinted with permission of the *Journal of Zoo and Wildlife Medicine*.)

Starting in the early 1990s, interest was developing among black-footed ferret conservationists for the identification of a safe and effective CDV vaccine to use in this endangered species. The potential to safeguard the black-footed ferret using a canarypox-vectored subunit vaccine led to a series of studies in Siberian polecats with the ultimate goal of applying this vaccine to the black-footed ferret; this work became a major focus starting in 1996. At the same time, it was recognized that this work could serve as a guide for other highly CDV-susceptible species. This vectored vaccine type, sometimes referred to as a type III recombinant vaccine (Van Kampen, 2001), used a canarypox vector to infect local (at the site of delivery) host cells, which then present HA and F antigens to T cells and macrophages, initiating cell-mediated and humoral responses (Schultz and Zuba, 2003). The canarypox vector was chosen because pox viruses do not use cell receptors for cell uptake during cellular endocytosis, the avian virus is avirulent at mammalian body temperatures, the pox genome is large enough to allow sizable vaccine-related gene substitutions, and pox vectors potentially reduce the risk of host genomic splicing (Tartaglia and others, 1992, 1993; Perkus and others, 1995a,b; Adams and others, 1997). Optimal recombinant vaccines are constructed to obtain high gene expression rates in host cells. Ideally, the immune system recognizes these cells and presents them to the humoral and cell-mediated arms of the immune system to develop a broad immune response with protective attributes somewhere between those of a modified-live vaccine and a KV vaccine (Schultz and Zuba, 2003). Advantages of this approach are that (1) no intact infectious agent is used, (2) pox virus products are more durable than modified-live CDV, and (3) adjuvants are not required. Vaccinated domestic cats (*Felis silvestris*) (Macy and Couto, 2001) appear to be at risk of developing injection site-associated sarcomas; this issue has also been raised with domestic ferrets, which appear at lower risk with recombinant vaccines (Merial Technical Services, oral commun., 2000). Another concern seen in domestic ferrets following repeated vaccination with approved modified-live products has been the increased risk of anaphylaxis (Fox and others, 1998). In one study surveying the risk of side-effects of vaccination in domestic ferrets, adverse reactions were reported approximately 5 percent of the time, particularly in older, previously vaccinated ferrets (Greenacre, 2003). This appears to be rarer with some products than others (Fox and others, 1998) and may be less likely with vectored vaccines although they have not been evaluated long enough to answer this question conclusively at this time. Repeated vaccination increased glomerular immune-complex deposition in mink receiving a multivalent vaccine that included CDV; unfortunately, the potential risk of glomerular disease was not studied (Newman and others, 2002). Recent anecdotal reports suggest that even the commercially available vectored CDV vaccine (PureVax® Ferret Distemper Vaccine; Merial, Inc., Athens, Ga.) is not without some risk in black-footed ferrets. Recently, several deaths in black-footed ferrets have been linked to its use in zoos (D. Garelle, oral commun., 2004).

Another important objective was to determine the efficacy of reCDV vaccine when delivered orally, so it could ultimately be used for wild black-footed ferrets in baits. Raboral V-RG® (Merial, Inc., Athens, Ga.), a vaccinia-vectored rabies subunit vaccine had been successfully packaged and broadcasted in baits to curtail fulminant rabies outbreaks in several wild carnivore populations (Fearneyhough and others, 1998; Hanlon and others, 1998; Olson and Werner, 1999). As demonstrated in domestic ferrets, vaccinia likely represents a better vector for oral administration than canarypox based on vaccination and challenge by enteric instillation (Welter and others, 1999). However, the risk of human infection when encountering the vaccinia vector remains of potential concern, particularly for immunocompromised individuals; a vectored-vaccine, bait-induced vaccinia infection was documented in a pet owner when she tried to remove a bait from her dog's mouth and was bitten in the process (Rupprecht and others, 2001). The appearance of a vaccinia strain from Brazil pathogenic to cattle and humans (Palca, 2005) may ignite a debate about the persistence of this virus, or of genetic constructs of this virus when used as a vector in the future.

Vaccination Effect on Humoral Immunity

In this study, pokeweed blastogenesis (pokeweed is a nonspecific B lymphocyte mitogen) was performed on blood samples from Siberian polecats collected immediately prior to and 14 days after a single reCDV vaccination ($10^{5.5}$ PFU) and coincidentally from unvaccinated saline control polecats.

Changes in blastogenesis responses of B lymphocytes in primary culture between vaccinates and controls were not statistically different (fig. 6). Hence, reCDV vaccination did not appear to cause significant suppression of B cell lines (immunosuppression) expected during sequelae of CDV modified-live vaccination and natural CDV infection.

In this study, we hypothesized that the immunosuppression associated with modified-live vaccination would not occur when using vectored CDV vaccines, a major

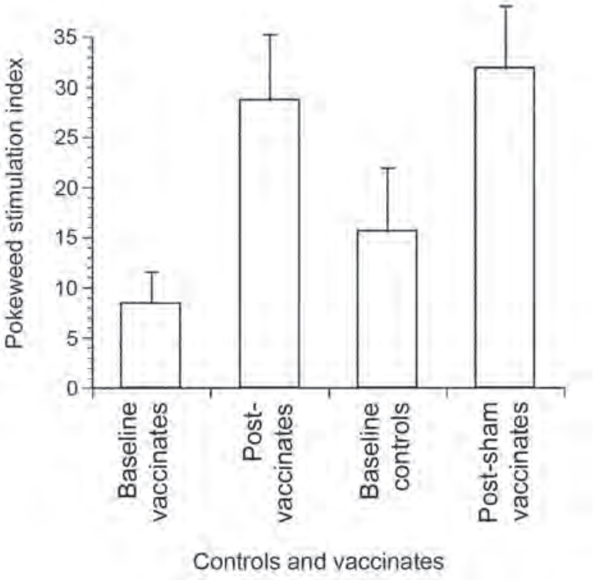


Figure 6. Pokeweed blastogenesis was performed on two samples of peripheral lymphocytes before and 14 days after canarypox-vectored recombinant canine distemper virus (reCDV) vaccination or saline control injections. The change in lymphocyte blastogenesis between controls and vaccinates was not significantly different and suggests that reCDV was not immunosuppressive as compared to live CDV exposure or modified-live virus vaccination.

advantage of the latter type. These results confirmed that the reCDV vaccine did not appear to cause a blunted B lymphocyte blastogenic response to pokeweed mitogen, typical of immunosuppression seen with modified-live CDV vaccines.

MLV Vaccine Boostering Following Vectored Vaccine

Onderstepoort strain origin genes for F and HA were used during construction of the reCDV vaccine and are expressed in Galaxy-D. To assess the potential for interference or synergy expected from use of reCDV followed by modified-live (Galaxy-D) vaccination, Siberian polecats that received a single reCDV dose ($10^{5.5}$ PFU) were subsequently boostered with Galaxy-D subcutaneously. These animals were challenged 61 days later. The timeline employed for blood sampling, vaccination, and challenge is depicted in fig. 3.

Five of five mixed sex Siberian polecats that received a single reCDV dose boostered with Galaxy-D survived challenge whereas six of six seronegative challenged controls succumbed.

This study in Siberian polecats showed that a single reCDV vaccination using the F and HA proteins from the Onderstepoort strain did not interfere with a single Galaxy-D vaccination that followed, in effect using the same antigens from this strain in both cases; likewise, during the challenge that followed, this combination provided 100 percent survival, and, in our hands, provided protection equivalent to that of a single Galaxy-D vaccination in domestic ferrets, as mentioned previously. The use of a MLV vaccine to booster the commercial reCDV vaccine (PureVax) is of interest to domestic ferret owners, and this practice has been shown to be effective in pet ferrets when using the currently USDA approved MLV (Fervac-D) vaccine (Merial Technical Services, oral commun., 2001). The production of low (blocking) titers and immune priming conferred by recombinant vectored vaccines may make them ideal candidates for MLV boostering that is expected to confer long-term immunity.

While not specifically tested, modified-live CDV boostering in black-footed ferrets suggests that modified-live vaccination following limited reCDV vaccination may be quite risky. Studies are in progress to establish the duration of titered immunity expected in black-footed ferrets over time following a primary two-vaccination series with PureVax (J. Kreeger, oral commun., 2004). Some investigators believe that three primary vaccinations will be warranted to provide a longer duration of immunity and higher protective titers (R. Montali, oral commun., 2003). Whether boostering with Galaxy-D or another relatively safe modified-live vaccine following some type of primary recombinant vaccination in black-footed ferrets will ever be worth the risk remains unclear. One important aspect of modified-live vaccination remains attractive; that is, the likely provision of life-long immunity in modified-live vaccinates. Immunity following a primary modified-live vaccination series with chick embryo attenuation was protective against lethal challenge at 6 years of age in mink and domestic ferrets (Burger and Gorham, 1964), and 5.5 years after similar vaccination in another domestic ferret study (Cabasso and Cox, 1953); this same result was reported in dogs 6.5 years after vaccination (L. Carmichael, personal commun., 1997, as reported by Gorham, 1999, p. 559). If repeated recombinant vectored vaccine vaccination does not confer life-long immunity, a trial to determine if MLV boostering following a full reCDV primary series may be warranted in black-footed ferrets destined for release, since it is highly unlikely they can be caught again for revaccination once in the wild. Alternatively, an effective oral baiting program with recombinant vaccine may be developed.

Vectored Vaccine Safety During Pregnancy

The timeline for vaccination, blood sampling, and challenge for evaluation of vectored vaccine safety in pregnant Siberian polecat females is shown in fig. 7 (upper timeline). Twelve treatment-randomized, unvaccinated Siberian polecat jills were compared to 12 reCDV vaccinates. Vaccination of CDV-naïve, reproductively intact polecat jills with a moderate reCDV dose ($10^{5.5}$ PFU subcutaneously) immediately prior to conception was followed by a second vaccine dose during the last 10 days of pregnancy.

Initial vectored vaccination had no significant effect on conception rates. Following a second vaccination at 29 days of gestation, birth outcomes such as litter size and kit rate of weight gain (measured from 17 to 35 days of age) were not significantly different from those in unvaccinated controls.

Canine distemper virus has been demonstrated to be capable of crossing the placental barrier of infected pregnant bitches and infecting their unborn puppies (Krakowka and others, 1974, 1977). Most reproductive-age bitches are either

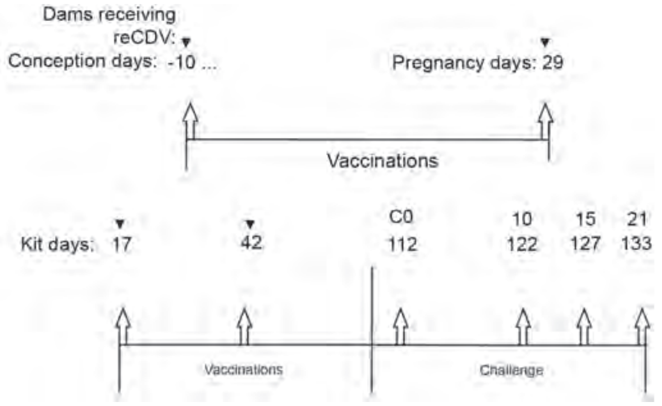


Figure 7. Timeline for the canarypox-vectored recombinant canine distemper virus (reCDV) immunization of Siberian polecat (*Mustela eversmannii*) dams to assess conception and pregnancy safety. Also shown is the timeline for vaccination of their kits in the passive immunity study. Triangles indicate days of vaccination. Arrows indicate days when blood samples were drawn.

vaccinated or exposed to CDV prior to pregnancy, conferring immunity; thus, it is likely that the potential for naïve dams of wild species or domestic canids to pass CDV transplacentally is underestimated (Krakowka and others, 1974), and the potential impact of CDV on reduced fecundity has not been well characterized in wild carnivores. Gorham (1999) conducted studies exploring the potential ill effects of vaccination before conception and during pregnancy employing a modified-live vaccine in mustelids. In those studies, modified-live vaccination influenced neither litter size nor apparent fertility; these results are similar to ours employing reCDV and suggest that high virus loads may be required to see transplacental disease.

Because the reCDV vaccine uses a novel vector, we tested the safety of this vaccine on reproductive polecat jills before conception, during pregnancy, and on kit growth 17–35 days postpartum as a prelude to vaccine use in reproductive black-footed ferrets. For 3 years, the National Black-footed Ferret Conservation Center has been vaccinating reproductive black-footed ferrets with PureVax starting several months prior to the breeding season. This practice has not caused any identifiable adverse effects on fecundity and overall production (P. Marinari, oral commun., 2004).

Vectored Vaccine Use in the Face of Passive Immunity

In 1997, 12 randomly selected Siberian polecat kits from mothers vaccinated twice with reCDV before conception and delivery (fig. 7, lower timeline) were themselves vaccinated at 4 and 6 weeks of age; kits received a standard challenge at 19 weeks of age.

All kits challenged at 19 weeks of age died with characteristic signs of CDV postchallenge. At this age, maternal protective immunity has disappeared in domestic ferrets (Gorham, 1999; Welter and others, 2000), suggesting that active immunization for CDV with reCDV (at $10^{5.5}$ PFU subcutaneously) in the presence of passive immunity, as tested in the present series, was without benefit.

Indirect evidence has suggested that antigen presentation to the cell-mediated arm of the immune system and particularly to T lymphocyte-induced cytotoxicity can lead to cell-mediated immunity independent of humoral responses (Siegrist and others, 1998a,b). It has been demonstrated in puppies (Taylor and others, 1994) that vectored vaccination with rabies glycoprotein results in active immunization in the face of blocking passive maternal antibodies. Here, we hypothesized that reCDV vaccine might actively protect young Siberian polecats postnatally even though they carried passive immune protection from circulating maternal antibodies generated against the same vaccine. According to this line of reasoning, active immunity would develop during postnatal vaccination with reCDV by independently augmenting active (mostly T cell-mediated) immunity. This possible application was attractive because maternal immunity typically blocks conventional vaccines during this period, and the actual trajectory of waning maternal immunity is unpredictable in mustelid kits (Gorham, 1999), leaving susceptible young unprotected. Welter and others (2000) challenged domestic ferrets at 12 weeks of age after parenteral vaccination with canarypox and vaccinia-vectored CDV vaccines for F and HA. In their study, vector-origin antigens had little effect on survival in early vaccinates, which was not significantly different from that of CDV-naïve controls. These results are similar to ours for the Siberian polecat, where early vaccinates, like CDV-naïve controls, succumbed to CDV during challenge. In their study, Welter and others (2000) attributed this vaccination failure to immaturity and nonresponsiveness of the immune system of the domestic ferret, a relatively altricial species. Our results support their observation; however, a lower dose of a canarypox-vectored vaccine was used in our study in Siberian polecats, complicating the final interpretation.

Canarypox cross-vaccination was not observed in unvaccinated Siberian polecats housed in adjacent cages. Thus, reCDV does not appear to be prone to cross-vaccination in this species. Similarly, reCDV vaccinated pregnant Siberian polecat jills adjacently caged with CDV and reCDV vector-naïve polecat jills never seroconverted following reCDV vaccination (J. Wimsatt, unpub. data., 1997).

Discussion

The ability of a vaccine to protect against differing CDV strains depends on how close the HA and F proteins are to the vaccine's Onderstepoort-origin proteins expressed by the vector. In this regard, Galaxy-D and the vectored (reCDV) vaccine are similar in the qualitative aspects of their protection. For the vectored vaccine, it is too early to assess the long-term effects of injecting canarypox into foreign species. In theory, the nature of recombinant vaccines and the limited antigens they express may require that they be updated more frequently to keep pace with strain changes, if other antigens can contribute to immune protection during modified-live infection and immunity development. If so, verified failure of antigenic protection with reCDV vaccines may potentially serve as a more exacting measure of evolving antigenic shifts in wild strains in the future.

In contrast to modified-live vaccination, vectored vaccine presentation to the mucosal membranes may yield different results from parenteral administration, reflecting limited vector invasiveness of mucosal surfaces, particularly in regards to the canarypox vector (Welter and others, 1999). Whether this will have a practical outcome, say in the heterogeneity of host responses across species following oral administration, remains to be determined. The long-term impact of live virus vectors and their potential to revert to virulence remains a matter of speculation, but careful monitoring is warranted, since poxviruses generally have the potential to mutate and adapt to new species. While replication of the canarypox virus in hosts appears to be minimal, the period of retention of the virus has not been as well characterized in varied species, and the large number of species receiving this vaccine leaves open the possibility of specific species predispositions and alterations in strain virulence over time, if persistence occurs. The recent emergence of a pathogenic variant of vaccinia virus may exemplify this concern (Palca, 2005).

What the Future May Hold

Considering the wide range of related morbilliviruses affecting diverse orders and classes of animals, and the demonstrated transfer of distemper and other morbilliviruses to bystander species (Stallknecht and others, 1991; Jacobson and others, 1992, 1997, 2001; Visser and others, 1993; Appel and Montali, 1994; Duignan and others, 1995; Richter and others, 1996; Karesh and others, 1997, 1999; Longbottom, 1997; Barrett, 1999; Jauniaux and others, 2000; Bossart and others, 2001; Lam and Chua, 2002; Johnson, 2003), the potential for cross-species movement and de novo creation of mutated variants of CDV seems high. For example, recent focus on HA variability among sympatric CDV strains (Gemma and others, 1996) suggests that commercial vaccine preparations may become inadequate for protection against CDV in the future (Mochizuki and others, 1999). However, caution is always warranted when documenting a vaccine failure because of the possibility of other causes. These other causes include incomplete dosing, genetic or ill-defined causes of host nonresponse (Leisewitz and others, 2001), administration during occult periods of host immunosuppression, and suboptimal product handling prior to use. Vaccine nonresponders have been documented for more than one canine disease (R. Schultz, oral commun., 2003).

A recent canine distemper outbreak at a zoo was associated with exposure to wild raccoons in the Chicago area (Lednicky and others, 2004). The appearance of this distinct strain has introduced some uncertainty about the ability of current commercial CDV vaccines to protect against new or emerging wildlife strains (Lednicky and others, 2004). Recent CDV disease outbreaks involving novel strains have raised the suspicion of vaccine failures although without controlled challenge studies these suspicions are difficult to prove (Bohm and others, 1989; Maes and others, 2003). Even so, this proposed causal relationship between novel strains, possibly from wildlife reservoirs, and the potential for vaccine failures has not been investigated adequately, employing careful ecological study techniques, modern molecular tools, and strain-specific challenge studies in vaccine-protected animals. An outbreak of naturally occurring CDV in black-footed ferrets highlights the need for safe and effective vaccines to protect them following reintroduction and as the threat continues into the future (Williams and others, 1988). Large cats and other carnivores would likely benefit as well (Blythe and others, 1983; Davidson and others, 1992; Appel and others, 1994; Harder and others, 1995; Roelke-Parker and others, 1996; Leisewitz and others, 2001).

The emergence of vaccine-resistant virus variants, like the analogous emergence of antibiotic-resistant bacteria, may be facilitated when vaccination is widely used and selection pressure is high. Even so, CDV vaccines have been surprisingly reliable over the last 50 years; this may relate to the observation that negative sense RNA viruses are less prone to recombine than other viruses (Chare and others, 2003).

Outbreaks of canine distemper in distant parts of the world have highlighted the significance of domestic and wildlife reservoirs as purveyors of distemper-induced disease worldwide (Bohm and others, 1989). Recent investigations surrounding CDV outbreaks in Japan (Mochizuki and others, 1999), Denmark (Blixenkrone-Moller and others, 1993), Poland (Jozwik and Frymus, 2002), and the United States (Lednicky and others, 2004) have brought into the focus the possible emergence of CDV strains no longer optimally immunized with commercial vaccine products. For the most part, such strains have shown characteristic heterogeneity in the HA gene, while the F component of current wild strains has remained surprisingly uniform across strains. This situation is analogous to using measles vaccination to cross-protect against CDV (Chalmers and Baxendale, 1994). When CDV passes across species, the possibility of variability at all sites, including the F protein gene, seems highly likely as new hosts tend to cause selection for greater virus diversity (Woolhouse and others, 2001). In related paramyxoviruses affecting other species, F gene heterogeneity has been noted and may influence species predilections, disease phenotypy, and vaccine efficacy in the future, especially under strong selection pressure (Collins and others, 1998; Ning and others, 2002; Ujvári and others, 2003).

The Promise of New Vaccine Strategies

A recent efficacy study using an adenovirus-vectored vaccine demonstrated the development of significant active immunity against CDV with the absence of mucosal immunity against the adenovirus vector in domestic puppies (Fischer and others, 2002). None of the other available vectored CDV vaccines are satisfactory for immunization of very young carnivores, and the adenovirus vector appears superior in this regard.

DNA vaccines are relatively safe, simple, and cheap to produce. They consist of DNA-encoding genes capable of producing vaccine antigens in host cells and mammalian promoters leading to selected gene expression (Liu, 2003). Recently, new DNA vaccines administered intramuscularly were shown to be highly effective against severe CDV challenge in mice (Sixt and others, 1998) and dogs (Fischer and others, 2003).

Unfortunately, nonparenteral methods of DNA vaccine and vectored vaccine delivery have low efficiency in producing a protective immune response. The low oral efficiency of the canarypox vector (Wimsatt and others, 2003) limits the potential use of commercial products now available

(Merial Technical Services, oral commun., 2004). Even so, a significant serological response was observed following oral administration (T. Vickers, oral commun., 2005) of two Pure-Vax vaccine doses at once in a recent study of Channel Island gray foxes (*Urocyon littoralis*) (Vickers and others, 2004). Vaccinia-vectored CDV constructs exist for research use (J. Taylor, oral commun., 1998). Vaccinia constructs appear to have greater enteric efficiency for bait delivery, as has been demonstrated during the use of Raboral V-RG in public health programs to vaccinate wild carnivores against rabies and experimentally with a vaccinia-vectored CDV vaccine (Welter and others, 1999). Mucosal delivery of DNA vaccines via new designer carriers will likely provide new opportunities for oral DNA vaccine delivery in the future (Hobson and others, 2003). With the advent of antiviral drugs, viral inhibitors of virus-host cell F are being developed to moderate paramyxovirus-induced disease progression, providing a new therapeutic approach (De Clercq, 2002).

The relatively homozygous (genetically depauperate) black-footed ferret is at risk of CDV-induced disease with the use of any currently available modified-live products. With the advent of designer vaccines for the concurrent delivery of immunostimulatory genes in concert with immunogens, the ability to stimulate the immune system (e.g., to express immunostimulatory levels of interleukin-6) while vaccinating will offer new possibilities in the future. Even the ability to correct an identified interleukin-6 deficiency in the black-footed ferret may be on the horizon through the use of gene therapy via vectored vaccine or naked DNA approaches. Such methods could eventually serve to enhance the resistance of this and other sensitive species to the ravages of infectious diseases, if germ line incorporation becomes practical.

References Cited

Adams, G.L., Ford, R.B., Gershwin, L.J., and Schultz, R.D., 1997, Recombinant vaccine technology: Compendium on Continuing Education for the Practicing Veterinarian, supplement, v. 19, p. 1–16.

Anonymous, 1978, Multiple sclerosis, canine distemper, and measles immunisation: Lancet, v. 1, p. 1204–1205.

Appel, M., and Robson, D.S., 1973, A microneutralization test for canine distemper virus: American Journal of Veterinary Research, v. 34, p. 1459–1463.

Appel, M.J., Glickman, L.T., Raine, C.S., and Tourtellotte, W.W., 1981, Canine viruses and multiple sclerosis: Neurology, v. 31, p. 944–949.

Appel, M.J., Reggiardo, C., Summers, B.A., Pearce-Kelling, S., Mare, C.J., Noon, T.H., Reed, R.E., Shively, J.N., and Orvell, C., 1991, Canine distemper virus infection and encephalitis in javelinas (collared peccaries): Archives of Virology, v. 119, p. 147–152.

Appel, M.J., and Summers, B.A., 1995, Pathogenicity of morbilliviruses for terrestrial carnivores: Veterinary Microbiology, v. 44, p. 187–191.

Appel, M.J., Yates, R.A., Foley, G.L., Bernstein, J.J., Santinelli, S., Spelman, L.H., Miller, L.D., Arp, L.H., Anderson, M., and Barr, M., 1994, Canine distemper epizootic in lions, tigers, and leopards in North America: Journal of Veterinary Diagnosis and Investigation, v. 6, p. 277–288.

Appel, M.J.G., and Montali, R.J., 1994, Canine distemper and emerging morbillivirus diseases in exotic species: American Association of Zoo Veterinarians, Annual Proceedings, p. 336–339.

Arjo, W.M., Gese, E.M., Bromley, C., Kozlowski, A., and Williams, E.S., 2003, Serologic survey for diseases in free-ranging coyotes (*Canis latrans*) from two ecologically distinct areas of Utah: Journal of Wildlife Diseases, v. 39, p. 449–455.

Axthelm, M.K., and Krakowka, S., 1998, Experimental old dog encephalitis (ODE) in a gnotobiotic dog: Veterinary Pathology, v. 35, p. 527–534.

Barrett, T., 1999, Morbillivirus infections, with special emphasis on morbilliviruses of carnivores: Veterinary Microbiology, v. 69, p. 3–13.

Barrett, T., Visser, I., Mamaev, L., Goatley, L., Van Bressem, M-F., and Osterhaus, A., 1993, Dolphin and porpoise morbilliviruses are genetically distinct from phocine distemper virus: Virology, v. 193, p. 1010–1021.

Bencsik, A., Malcus, C., Akaoka, H., Giraudon, P., Belin, M.F., and Bernard, A., 1996, Selective induction of cytokines in mouse brain infected with canine distemper virus—structural, cellular and temporal expression: Journal of Neuroimmunology, v. 65, p. 1–9.

Blixenkrone-Moller, M., Svansson, V., Have, P., Orvell, C., Appel, M., Pedersen, I.R., Dietz, H.H., and Henriksen, P., 1993, Studies on manifestations of canine distemper virus infection in an urban dog population: Veterinary Microbiology, v. 37, p. 163–173.

Blythe, L.L., Schmitz, J.A., Roelke, M., and Skinner, S., 1983, Chronic encephalomyelitis caused by canine distemper virus in a Bengal tiger: Journal of the American Veterinary Medical Association, v. 183, p. 1159–1162.

Bohm, J., Blixenkrone-Moller, M., and Lund, E., 1989, A serious outbreak of canine distemper among sled-dogs in northern Greenland: Arctic Medical Research, v. 48, p. 195–203.

Bossart, K.N., Wang, L.F., Eaton, B.T., and Broder, C.C., 2001, Functional expression and membrane fusion tropism of the envelope glycoproteins of Hendra virus: Virology, v. 290, p. 121–135.

Bronson, E., Denver, M., Karim, B., Fitzgerald, S., Wise, A.G., and Maes, R., 2003, Vaccine-induced canine distemper virus infection in a lesser panda (*Ailurus fulgens fulgens*) three years following last vaccination: American Association of Zoo Veterinarians, Annual Proceedings, p. 185–186.

Burger, D., and Gorham, J.R., 1964, Response of ferrets and mink to vaccination with chicken embryo-adapted distemper virus: Archiv Gesamte Virusforsch, v. 15, p. 449–461.

Bush, M., Montali, R.J., Brownstein, D., James, A.E., Jr., and Appel, M.J., 1976, Vaccine-induced canine distemper in a lesser panda: Journal of the American Veterinary Medical Association, v. 169, p. 959–960.

Cabasso, V.J., and Cox, H.R., 1953, Onset of resistance and duration of immunity to distemper in ferrets following a single injection of avianized distemper vaccine: Veterinary Medicine, v. 48, p. 147–150.

Carpenter, J.W., Appel, M.J., Erickson, R.C., and Novilla, M.N., 1976, Fatal vaccine-induced canine distemper virus infection in black-footed ferrets: Journal of the American Veterinary Medical Association, v. 169, p. 961–964.

Carpenter, M.A., Appel, M.J., Roelke-Parker, M.E., Munson, L., Hofer, H., East, M., and O’Brien, S.J., 1998, Genetic characterization of canine distemper virus in Serengeti carnivores: Veterinary Immunology and Immunopathology, v. 65, p. 259–266.

Cartwright, E.J., Gordon, M.T., Freemont, A.J., Anderson, D.C., and Sharpe, P.T., 1993, Paramyxoviruses and Paget’s disease: Journal of Medical Virology, v. 40, p. 133–141.

Chalmers, W.S., and Baxendale, W., 1994, A comparison of canine distemper vaccine and measles vaccine for the prevention of canine distemper in young puppies: Veterinary Record, v. 135, p. 349–353.

Chare, E.R., Gould, E.A., and Holmes, E.C., 2003, Phylogenetic analysis reveals a low rate of homologous recombination in negative-sense RNA viruses: Journal of General Virology, v. 84, p. 2691–2703.

Collins, M.S., Franklin, S., Strong, I., Meulemans, G., and Alexander, D.J., 1998, Antigenic and phylogenetic studies on a variant Newcastle disease virus using anti-fusion protein monoclonal antibodies and partial sequencing of the F protein gene: Avian Pathology, v. 27, p. 90–96.

Cook, S.D., Blumberg, B., and Dowling, P.C., 1986, Potential role of paramyxoviruses in multiple sclerosis: Neurologic Clinics, v. 4, p. 303–319.

Cypher, B.L., Scrivner, J.H., Hammer, K.L., and O’Farrell, T.P., 1998, Viral antibodies in coyotes from California: Journal of Wildlife Diseases, v. 34, p. 259–264.

Davidson, W.R., Nettles, V.F., Hayes, L.E., Howerth, E.W., and Couvillion, C.E., 1992, Diseases diagnosed in gray foxes (*Urocyon cinereoargenteus*) from the southeastern United States: Journal of Wildlife Diseases, v. 28, p. 28–33.

De Clercq, E., 2002, Highlights in the development of new antiviral agents: Mini Reviews in Medicinal Chemistry, v. 2, p. 163–175.

De Keyser, J., Wilczak, N., Walter, J.H., and Zurbriggen, A., 2001, Disappearance of beta2-adrenergic receptors on astrocytes in canine distemper encephalitis—possible implications for the pathogenesis of multiple sclerosis: Neuroreport, v. 12, p. 191–194.

Dhurandhar, N.V., 2001, Infectobesity—obesity of infectious origin: Journal of Nutrition, v. 131, p. 2794S–2797S.

Duignan, P.J., House, C., Geraci, J.R., Duffy, N., Rima, B.K., Walsh, M.T., Early, G., St. Aubin, D.J., Sadove, S., Koopman, H., and Rhinehart, H., 1995, Morbillivirus infection in cetaceans of the western Atlantic: Veterinary Microbiology, v. 44, p. 241–249.

Dunbar, M.R., Cunningham, M.W., and Roof, J.C., 1998, Seroprevalence of selected disease agents from free-ranging black bears in Florida: Journal of Wildlife Diseases, v. 34, p. 612–619.

Dyken, P.R., 2001, Neuroprogressive disease of post-infectious origin—a review of a resurging subacute sclerosing panencephalitis (SSPE): Mental Retardation and Developmental Disabilities Research Reviews, v. 7, p. 217–225.

Etchart, N., Desmoulins, P-O., Chemin, K., Maliszewski, C., Dubois, B., Wild, F., and Kaiserlian, D., 2001, Dendritic cells recruitment and in vivo priming of $CD8^+$ CTL induced by a single topical or transepithelial immunization via the buccal mucosa with measles virus nucleoprotein: Journal of Immunology, v. 167, p. 384–391.

Evans, M.B., Bunn, T.O., Hill, H.T., and Platt, K.B., 1991, Comparison of in vitro replication and cytopathology caused by strains of canine distemper virus of vaccine and field origin: Journal of Veterinary Diagnostic Investigation, v. 3, p. 127–132.

Farrell, R.K., Skinner, S.F., Gorham, J.R., and Lauerman, L.H., 1971, The aerosol and subcutaneous administration of attenuated egg adapted distemper vaccine to ferret kits from distemper immune females: Research in Veterinary Sciences, v. 12, p. 392–393.

Fearneyhough, M.G., Wilson, P.J., Clark, K.A., Smith, D.R., Johnston, D.H., Hicks, B.N., and Moore, G.M., 1998, Results of an oral rabies vaccination program for coyotes:

Journal of the American Veterinary Medical Association, v. 212, p. 498–502.

Fischer, L., Tronel, J.P., Minke, J., Barzu, S., Baudu, P., and Audonnet, J.C., 2003, Vaccination of puppies with a lipid-formulated plasmid vaccine protects against a severe canine distemper virus challenge: Vaccine, v. 21, p. 1099–1102.

Fischer, L., Tronel, J.P., Pardo-David, C., Tanner, P., Colombet, G., Minke, J., and Audonnet, J.C., 2002, Vaccination of puppies born to immune dams with a canine adenovirus-based vaccine protects against a canine distemper virus challenge: Vaccine, v. 20, p. 3485–3497.

Fox, J., Pearson, R., and Gorham, J., 1998, Viral diseases, *in* Fox, J.G., ed., Biology and diseases of the ferret (2d ed.): Baltimore, Md., Williams and Wilkins, Chap. 15, p. 355–360.

Fraser, W.D., 1997, Paget's disease of bone: Current Opinions in Rheumatology, v. 9, p. 347–354.

Friedrichs, W.E., Reddy, S.V., Bruder, J.M., Cundy, T., Cornish, J., Singer, F.R., and Roodman, G.D., 2002, Sequence analysis of measles virus nucleocapsid transcripts in patients with Paget's disease: Journal of Bone and Mineral Research, v. 17, p. 145–151.

Garg, R.K., 2002, Subacute sclerosing panencephalitis: Postgraduate Medical Journal, v. 78, p. 63–70.

Gemma, T., Watari, T., Akiyama, K., Miyashita, N., Shin, Y.S., Iwatsuki, K., Kai, C., and Mikami, T., 1996, Epidemiological observations on recent outbreaks of canine distemper in Tokyo area: Journal of Veterinary Medical Sciences, v. 58, p. 547–550.

Gese, E.M., Schultz, R.D., Johnson, M.R., Williams, E.S., Crabtree, R.L., and Ruff, R.L., 1997, Serological survey for diseases in free-ranging coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: Journal of Wildlife Diseases, v. 33, p. 47–56.

Gese, E.M., Schultz, R.D., Rongstad, O.J., and Andersen, D.E., 1991, Prevalence of antibodies against canine parvovirus and canine distemper virus in wild coyotes in southeastern Colorado: Journal of Wildlife Diseases, v. 27, p. 320–323.

Gorham, J.R., 1966, Duration of vaccination immunity and the influence on subsequent prophylaxis: Journal of the American Veterinary Medical Association, v. 149, p. 699–704.

Gorham, J.R., 1999, Some experiments and field observations of distemper in mink and ferrets: Advances in Veterinary Medicine, v. 41, p. 557–570.

Greenacre, C.B., 2003, Incidence of adverse events in ferrets vaccinated with distemper or rabies vaccine: 143 cases (1995–2001): Journal of the American Veterinary Medical Association, v. 223, p. 663–665.

Greene, C.E., and Appel, M.J.G., 1998, Canine distemper, *in* Greene, C.E., Infectious diseases of the dog and cat: Philadelphia, Pa., W.B. Saunders, Chap. 3, p. 9–22.

Grinder, M., and Krausman, P.R., 2001, Morbidity-mortality factors and survival of an urban coyote population in Arizona: Journal of Wildlife Diseases, v. 37, p. 312–317.

Grone, A., Fonfara, S., and Baumgartner, W., 2002, Cell type-dependent cytokine expression after canine distemper virus infection: Viral Immunology, v. 15, p. 493–505.

Guo, W., Evermann, J.F., Foreyt, W.J., Knowlton, F.F., and Windberg, L.A., 1986, Canine distemper virus in coyotes—a serologic survey: Journal of the American Veterinary Medical Association, v. 189, p. 1099–1100.

Hagen, K.W., Goto, H., and Gorham, J.R., 1970, Distemper vaccine in pregnant ferrets and mink: Research in Veterinary Sciences, v. 11, p. 458–460.

Halbrooks, R.D., Swango, L.J., Schnurrenberger, P.R., Mitchell, F.E., and Hill, E.P., 1981, Response of grey foxes to modified-live virus canine distemper vaccines: Journal of the American Veterinary Medical Association, v. 179, p. 1170–1174.

Hall, W.W., Imagawa, D.T., and Choppin, P.W., 1979, Immunological evidence for the synthesis of all canine distemper virus polypeptides in chronic neurological diseases in dogs—chronic distemper and old dog encephalitis differ from SSPE in man: Virology, v. 98, p. 283–287.

Hanlon, C.A., Niezgoda, M., Hamir, A.N., Schumacher, C., Koprowski, H., and Rupprecht, C.E., 1998, First North American field release of vaccinia-rabies glycoprotein recombinant virus: Journal of Wildlife Diseases, v. 34, p. 228–239.

Harder, T.C., Kenter, M., Appel, M.J., Roelke-Parker, M.E., Barrett, T., and Osterhaus, A.D., 1995, Phylogenetic evidence of canine distemper virus in Serengeti's lions: Vaccine, v. 13, p. 521–523.

Harrus, S., Waner, T., Aizenberg, I., Safra, N., Mosenco, A., Radoshitsky, M., and Bark, H., 2002, Development of hypertrophic osteodystrophy and antibody response in a litter of vaccinated Weimaraner puppies: Journal of Small Animal Practice, v. 43, p. 27–31.

Hashimoto, M., Une, Y., and Mochizuki, M., 2001, Hemagglutinin genotype profiles of canine distemper virus from domestic dogs in Japan: Archives of Virology, v. 146, p. 149–155.

Hernan, M.A., Zhang, S.M., Lipworth, L., Olek, M.J., and Ascherio, A., 2001, Multiple sclerosis and age at infection with common viruses: Epidemiology, v. 12, p. 301–306.

Hobson, P., Barnfield, C., Barnes, A., and Klavinskis, L.S., 2003, Mucosal immunization with DNA vaccines: Methods, v. 31, p. 217–224.

Hoyland, J.A., Dixon, J.A., Berry, J.L., Davies, M., Selby, P.L., and Mee, A.P., 2003, A comparison of in situ hybridisation, reverse transcriptase-polymerase chain reaction (RT-PCR) and in situ-RT-PCR for the detection of canine distemper virus RNA in Paget's disease: Journal of Virological Methods, v. 109, p. 253–259.

Ikeda, Y., Nakamura, K., Miyazawa, T., Chen, M.C., Kuo, T.F., Lin, J.A., Mikami, T., Kai, C., and Takahashi, E., 2001, Seroprevalence of canine distemper virus in cats: Clinical Diagnostics and Laboratory Immunology, v. 8, p. 641–644.

Itakura, C., Nakamura, K., Nakatsuka, J., and Goto, M., 1979, Distemper infection in lesser pandas due to administration of a canine distemper live vaccine: Nippon Juigaku Zasshi, v. 41, p. 561–566.

Jacobson, E.R., Adams, H.P., Geisbert, T.W., Tucker, S.J., Hall, B.J., and Homer, B.L., 1997, Pulmonary lesions in experimental ophidian paramyxovirus pneumonia of Aruba Island rattlesnakes, *Crotalus unicolor*: Veterinary Pathology, v. 34, p. 450–459.

Jacobson, E.R, Gaskin, J.M., Wells, S., Bowler, K., and Schumacher, J., 1992, Epizootic of ophidian paramyxovirus in a zoological collection—pathological, microbiological, and serological findings: Journal of Zoo and Wildlife Medicine, v. 23, p. 318–327.

Jacobson, E.R., Origgi, F., Pessier, A.P., Lamirande, E.W., Walker, I., Whitaker, B., Stalis, I.H., Nordhausen, R., Owens, J.W., and Nichols, D.K., 2001, Paramyxovirus infection in caiman lizards (*Draecaena guianensis*): Journal of Veterinary Diagnostic Investigation, v. 13, p. 143–151.

Jauniaux, T., Charlier, G., Desmecht, M., Haelters, J., Jacques, T., Losson, B., Van Gompel, J., Tavernier, J., and Coignoul, F., 2000, Pathological findings in two fin whales (*Balaenoptera physalus*) with evidence of morbillivirus infection: Journal of Comparative Pathology, v. 123, p. 198–201.

Johnson, R.T., 2003, Emerging viral infections of the nervous system: Journal of NeuroVirology, v. 9, p. 140–147.

Jozwik, A., and Frymus, T., 2002, Natural distemper in vaccinated and unvaccinated dogs in Warsaw: Journal of Veterinary Medicine, Series B, Infectious Diseases and Veterinary Public Health, v. 49, p. 413–414.

Karesh, W.B., del Campo, A., Braselton, W.E., Puche, H., and Cook, R.A., 1997, Health evaluation of free-ranging and hand-reared macaws (*Ara* spp.) in Peru: Journal of Zoo and Wildlife Medicine, v. 28, p. 368–377.

Karesh, W.B., Uhart, M.M., Frere, E., Gandini, P., Braselton, W.E., Puche, H., and Cook, R.A., 1999, Health evaluation of free-ranging rockhopper penguins (*Eudyptes chrysocomes*) in Argentina: Journal of Zoo and Wildlife Medicine, v. 30, p. 25–31.

Kennedy, S., Kuiken, T., Jepson, P.D., Deaville, R., Forsyth, M., Barrett, T., van de Bildt, M.W., Osterhaus, A.D., Eybatov, T., and Duck, C., 2000, Mass die-off of Caspian seals caused by canine distemper virus: Emerging Infectious Diseases, v. 6, p. 637–639.

Krakowka, S., 1982, Mechanisms of in vitro immunosuppression in canine distemper virus infection: Journal of Clinical Laboratory Immunology, v. 8, p. 187–196.

Krakowka, S., Confer, A., and Koestner, A., 1974, Evidence for transplacental transmission of canine distemper virus—two case reports: American Journal of Veterinary Research, v. 35, p. 1251–1253.

Krakowka, S., Hoover, E.A., Koestner, A., and Ketring, K., 1977, Experimental and naturally occurring transplacental transmission of canine distemper virus: American Journal of Veterinary Research, v. 38, p. 919–922.

Krakowka, S., Ringler, S.S., Lewis, M., Olsen, R.G., and Axthelm, M.K., 1987, Immunosuppression by canine distemper virus—modulation of in vitro immunoglobulin synthesis, interleukin release and prostaglandin E2 production: Veterinary Immunology and Immunopathology, v. 15, p. 181–201.

Lam, S.K., and Chua, K.B., 2002, Nipah virus encephalitis outbreak in Malaysia: Clinical Infectious Diseases, v. 34, Suppl. 2, p. S48–S51.

Lednicky, J., Dubach, J., Kinsel, M.J., Meehan, T.P., Bocchetta, M., Hungerford, L.L., Sarich, N.A., Witecki, K.E., Braid, M.D., Pedrak, C., and Houde, C.M., 2004, Genetically distant canine distemper virus lineages have recently caused epizootics with somewhat different characteristics in raccoons living around a large suburban zoo in the USA: Virology Journal, v. 1, http://www.virologyj.com/content/1/1/2.

Leisewitz, A.L., Carter, A., Van Vuuren, M., and Van Blerk, L., 2001, Canine distemper infections, with special reference to South Africa, with a review of the literature: Journal of South African Veterinary Association, v. 72, p. 127–136.

Liashenko, V.A., Krasnova, V.P., and Youminova, N.V., 1999, Measles IgA in the nasal washings of adult volunteers and children immunized intranasally with measles vaccine L-16: Human Antibodies, v. 9, p. 143–148.

Lincoln, S.D., Gorham, J.R., Ott, R.L., and Hegreberg, G.A., 1971, Etiologic studies of old dog encephalitis. I. Demonstration of canine distemper viral antigen in the brain in two cases: Veterinary Pathology, v. 8, p. 1–8.

Liu, M.A., 2003, DNA vaccines—a review: Journal of Internal Medicine, v. 253, p. 402–410.

Longbottom, H., 1997, Emerging infectious diseases: Communicable Diseases Intelligence, v. 21, p. 89–93.

Macy, D.W., and Couto, C.G., 2001, Prevention and treatment of injection-site sarcomas: Journal of Feline Medicine and Surgery, v. 3, p. 169–170.

Maes, R.K., Wise, A.G., Fitzgerald, S.D., Ramudo, A., Kline, J., Vilnis, A., and Benson, C., 2003, A canine distemper outbreak in Alaska—diagnosis and strain characterization using sequence analysis: Journal of Veterinary Diagnostic Investigation, v. 15, p. 213–220.

Mee, A.P., Dixon, J.A., Hoyland, J.A., Davies, M., Selby, P.L., and Mawer, E.B., 1998, Detection of canine distemper virus in 100% of Paget's disease samples by in situ-reverse transcriptase-polymerase chain reaction: Bone, v. 23, p. 171–175.

Mee, A.P., Gordon, M.T., May, C., Bennett, D., Anderson, D.C., and Sharpe, P.T., 1993, Canine distemper virus transcripts detected in the bone cells of dogs with metaphyseal osteopathy: Bone, v. 14, p. 59–67.

Meertens, N., Stoffel, M.H., Cherpillod, P., Wittek, R., Vandevelde, M., and Zurbriggen, A., 2003, Mechanism of reduction of virus release and cell-cell fusion in persistent canine distemper virus infection: Acta Neuropathologica, v. 106, p. 303–310.

Mochizuki, M., Hashimoto, M., Hagiwara, S., Yoshida, Y., and Ishiguro, S., 1999, Genotypes of canine distemper virus determined by analysis of the hemagglutinin genes of recent isolates from dogs in Japan: Journal of Clinical Microbiology, v. 37, p. 2936–2942.

Montali, R.J., Bartz, C.R., Teare, J.A., Allen, J.T., Appel, M.J., and Bush, M., 1983, Clinical trials with canine distemper vaccines in exotic carnivores: Journal of the American Veterinary Medical Association, v. 183, p. 1163–1167.

Montali, R.J., Tell, L., Bush, M., Cambre, R.C., Kenny, D., Sutherland-Smith, M., and Appel, M.J.G., 1994, Vaccination against canine distemper in exotic carnivores—successes and failures: American Association of Zoo Veterinarians, Annual Proceedings, p. 340–344.

Moro, L., de Sousa Martins, A., de Moraes Alves, C., de Araujo Santos, F.G., dos Santos Nunes, J.E., Carneiro, R.A., Carvalho, R., and Vasconcelos, A.C., 2003a, Apoptosis in canine distemper: Archives of Virology, v. 148, p. 153–164.

Moro, L., Martins, A.S., Alves, C.M., Santos, F.G., Del Puerto, H.L., and Vasconcelos, A.C., 2003b, Apoptosis in the cerebellum of dogs with distemper: Journal of Veterinary Medicine, Part B, Infectious Diseases of Veterinary Public Health, v. 50 p. 221–225.

Newman, S.J., Johnson, R., Sears, W., and Wilcock, B., 2002, Investigation of repeated vaccination as a possible cause of glomerular disease in mink: Canadian Journal of Veterinary Research, v. 66, p. 158–164.

Ning, X., Ayata, M., Kimura, M., Komase, K., Furukawa, K., Seto, T., Ito, N., Shingai, M., Matsunaga, I., and Yamano, T., 2002, Alterations and diversity in the cytoplasmic tail of the fusion protein of subacute sclerosing panencephalitis virus strains isolated in Osaka, Japan: Virus Research, v. 86, p. 123–131.

Noon, T.H., Heffelfinger, J.R., Olding, R.J., Wesche, S.L., and Reggiardo, C., 2003, Serologic survey for antibodies to canine distemper virus in collared peccary (*Tayassu tajacu*) populations in Arizona: Journal of Wildlife Diseases, v. 39, p. 221–223.

O'Brien, S.J., Martenson, J.S., Eichelberger, M.A., Thorne, E.T., and Wright, F., 1989, Genetic variation and molecular systematics of the black-footed ferret, *in* Seal, U.S., Thorne, E.T., Bogan, M.A., and Anderson, S.H., eds., Conservation biology and the black-footed ferret: New Haven, Conn., Yale University Press, p. 21–33.

Ogra, P.L., Fishaut, M., and Gallagher, M.R., 1980, Viral vaccination via the mucosal routes: Reviews of Infectious Diseases, v. 2, p. 352–369.

Olson, C.A., and Werner, P.A., 1999, Oral rabies vaccine contact by raccoons and nontarget species in a field trial in Florida: Journal of Wildlife Diseases, v. 35, p. 687–695.

Palca, J., 2005, Flu-like disease in Brazil puzzles experts: NPR, Nov. 10, 2005.

Paoletti, E., Tartaglia, J., and Cox, W.I., 1993, Immunotherapeutic strategies for cancer using poxvirus vectors: Annals of the New York Academy of Sciences, v. 690, p. 292–300.

Paoletti, E., Tartaglia, J., and Taylor, J., 1994, Safe and effective poxvirus vectors—NYVAC and ALVAC: Development of Biological Standards, v. 82, p. 65–69.

Paoletti, E., Taylor, J., Meignier, B., Meric, C., and Tartaglia, J., 1995, Highly attenuated poxvirus vectors—NYVAC, ALVAC and TROVAC: Development of Biological Standards, v. 84, p. 159–163.

Perkus, M.E., Tartaglia, J., and Paoletti, E., 1995a, Poxvirus-based vaccine candidates for cancer, AIDS, and other infectious diseases: Journal of Leukocyte Biology, v. 58, p. 1–13.

Perkus, M.E., Taylor, J., Tartaglia, J., Pincus, S., Kauffman, E.B., Tine, J.A., and Paoletti, E., 1995b, Live attenuated vaccinia and other poxviruses as delivery systems—public health issues: Annals of the New York Academy of Sciences, v. 754, p. 222–233.

Pincus, S., Tartaglia, J., and Paoletti, E., 1995, Poxvirus-based vectors as vaccine candidates: Biologicals, v. 23, p. 159–164.

Pollack, J.D., 2001, Caspian seal die-off is caused by canine distemper virus: Trends in Microbiology, v. 9, p. 108.

Povey, R.C., 1986, Persistent viral infection. The carrier state: Veterinary Clinics of North America, Small Animal Practice, v. 16, p. 1075–1095.

Richter, G.A., Homer, B.L., Moyer, S.A., Williams, D.S., Scherba, G., Tucker, S.J., Hall, B.J., Pedersen, J.C., and Jacobson, E.R., 1996, Characterization of paramyxoviruses isolated from three snakes: Virus Research, v. 43, p. 77–83.

Rima, B.K., Baczko, K., Imagawa, D.T., and ter Meulen, V., 1987, Humoral immune response in dogs with old dog encephalitis and chronic distemper meningo-encephalitis: Journal of General Virology, v. 68, p. 1723–1735.

Rockborn, G., 1957, Viraemia and neutralizing antibodies in naturally acquired distemper in dogs: Archiv Gesamte Virusforsch, v. 7, p. 183–190.

Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O’Brien, S.J., Pospischil, A., Hofmann-Lehmann, R., and Lutz, H., 1996, A canine distemper virus epidemic in Serengeti lions (*Panthera leo*): Nature, v. 379, p. 441–445.

Rupprecht, C.E., Blass, L., Smith, K., Oriciari, L.A., Niezgoda, M., Whitfield, S.G., Gibbons, R.V., Guerra, M., and Hanlon, C.A., 2001, Human infection due to recombinant vaccinia-rabies glycoprotein virus: New England Journal of Medicine, v. 345, p. 582–586.

Rzezutka, A., and Mizak, B., 2002, Application of N-PCR for diagnosis of distemper in dogs and fur animals: Veterinary Microbiology, v. 88, p. 95–103.

Saliki, J.T., Cooper, E.J., and Gustavson, J.P., 2002, Emerging morbillivirus infections of marine mammals—development of two diagnostic approaches: Annals of the New York Academy of Sciences, v. 969, p. 51–59.

Schlender, J., Schnorr, J-J., Spielhofer, P., Cathomen, T., Cattaneo, R., Billeter, M., ter Meulen, V., and Schneider-Schaulies, S., 1996, Interaction of measles virus glycoproteins with the surface of uninfected peripheral blood lymphocytes induces immunosuppression *in vitro*: Proceedings of the National Academy of Sciences, v. 93, p. 13194–13199.

Schneider-Schaulies, J., ter Meulen, V., and Schneider-Schaulies, S., 2003, Measles infection of the central nervous system: Journal of NeuroVirology, v. 9, p. 247–252.

Schultz, R.D., 1976, Failure of attenuated canine distemper virus (Rockborn strain) to suppress lymphocyte blastogenesis in dogs: Cornell Veterinarian, v. 66, p. 27–31.

Schultz, R., and Zuba, J., 2003, Understanding the basic principles and practical aspects of vaccinology: American Association of Zoo Veterinarians, Annual Proceedings, p. 162–178.

Siegrist, C.A., Barrios, C., Martinez, X., Brandt, C., Berney, M., Cordova, M., Kovarik, J., and Lambert, P.H., 1998a, Influence of maternal antibodies on vaccine responses—inhibition of antibody but not T cell responses allows successful early prime-boost strategies in mice: European Journal of Immunology, v. 28, p. 4138–4148.

Siegrist, C.A., Saddallah, F., Tougne, C., Martinez, X., Kovarik, J., and Lambert, P.H., 1998b, Induction of neonatal TH1 and CTL responses by live viral vaccines—a role for replication patterns within antigen presenting cells?: Vaccine, v. 16, p. 1473–1478.

Sixt, N., Cardoso, A., Vallier, A., Fayolle, J., Buckland, R., and Wild, T.F., 1998, Canine distemper virus DNA vaccination induces humoral and cellular immunity and protects against a lethal intracerebral challenge: Journal of Virology, v. 72, p. 8472–8476.

Stallknecht, D.E., Senne, D.A., Zwank, P.J., Shane, S.M., and Kearney, M.T., 1991, Avian paramyxoviruses from migrating and resident ducks in coastal Louisiana: Journal of Wildlife Diseases, v. 27, p. 123–128.

Stern, L.B., Greenberg, M., Gershoni, J.M., and Rozenblatt, S., 1995, The hemagglutinin envelope protein of canine distemper virus (CDV) confers cell tropism as illustrated by CDV and measles virus complementation analysis: Journal of Virology, v. 69, p. 1661–1668.

Stoskopf-Kennedy, S., Horsman, A.E., and Burns, R.B., 1997, Absence of interleukin-6 (IL-6) expression in the black-footed ferret (*Mustela nigripes*) [abs.]: 7th Congress of the International Society of Developmental and Comparative Immunology: Williamsburg, Va., College of William and Mary, p. 217.

Sutherland-Smith, M.R., Rideout, B.A., Mikolon, A.B., Appel, M.J., Morris, P.J., Shima, A.L., and Janssen, D.J., 1997, Vaccine-induced canine distemper in European mink, *Mustela lutreola*: Journal of Zoo and Wildlife Medicine, v. 28, p. 312–318.

Svansson, V., Blixenkrone-Moller, M., Skirnisson, K., Have, P., Heje, N.I., Nielsen, J., and Lund, E., 1993, Infection studies with canine distemper virus in harbour seals: Archives of Virology, v. 131, p. 349–359.

Tartaglia, J., Cox, W.I., Taylor, J., Perkus, M., Riviere, M., Meignier, B., and Paoletti, E., 1992, Highly attenuated poxvirus vectors: AIDS Research and Human Retroviruses, v. 8, 1445–1447.

Tartaglia, J., Pincus, S., and Paoletti, E., 1990, Poxvirus-based vectors as vaccine candidates: Critical Reviews in Immunology, v. 10, p. 13–30.

Tartaglia, J., Taylor, J., Cox, W.I., Audonnet, J., Perkus, M.E., Paoletti, E., Radaelli, A., Morghen, C., Meignier, B., and Riviere, M., 1993, Novel poxvirus strains as research tools and vaccine vectors, *in* Koff, W.C., Wong-Staal, F., and Kennedy, R.C., eds., AIDS Research Reviews: New York, Marcel-Dekker, Inc., p. 361–378.

Taylor, J., Tartaglia, J., Riviere, M., Duret, C., Languet, B., Chappuis, G., and Paoletti, E., 1994, Applications of canarypox (ALVAC) vectors in human and veterinary vaccination: Development of Biological Standards, v. 82, p. 131–135.

Tipold, A., Moore, P., Zurbriggen, A., Burgener, I., Barben, G., and Vandevelde, M., 1999, Early T cell response in the central nervous system in canine distemper virus infection: Acta Neuropathologica, v. 97, p. 45–56.

Tobler, L.H., and Imagawa, D.T., 1984, Mechanism of persistence with canine distemper virus—difference between a laboratory strain and an isolate from a dog with chronic neurological disease: Intervirology, v. 21, p. 77–86.

Truyen, U., Muller, T., Heidrich, R., Tackmann, K., and Carmichael, L.E., 1998, Survey on viral pathogens in wild red foxes (*Vulpes vulpes*) in Germany with emphasis on parvoviruses and analysis of a DNA sequence from a red fox parvovirus: Epidemiology and Infection, v. 121, p. 433–440.

Ujvári, D., Wehmann, E., Kaleta, E.F., Werner, O., Savic, V., Nagy, É., Czifra, G., and Lomniczi, B., 2003, Phylogenetic analysis reveals extensive evolution of avian paramyxovirus type 1 strains of pigeons (*Columba livia*) and suggests multiple species transmission: Virus Research, v. 96, p. 63–73.

van de Bildt, M.W., Kuiken, T., Visee, A.M., Lema, S., Fitzjohn, T.R., and Osterhaus, A.D., 2002, Distemper outbreak and its effect on African wild dog conservation: Emerging Infectious Diseases, v. 8, p. 211–213.

Vandevelde, M., Kristensen, B., Braund, K.G., Greene, C.E., Swango, L.J., and Hoerlein, B.F., 1980, Chronic canine distemper virus encephalitis in mature dogs: Veterinary Pathology, v. 17, p. 17–28.

Vandevelde, M., and Zurbriggen, A., 1995, The neurobiology of canine distemper virus infection: Veterinary Microbiology, v. 44, p. 271–280.

Van Kampen, K.R., 2001, Recombinant vaccine technology in veterinary medicine: Veterinary Clinics of North America, Small Animal Practice, v. 31, p. 535–538.

Verlaeten, O., Griffond, B., Khuth, S.T., Giraudon, P., Akaoka, H., Belin, M.F., Fellmann, D., and Bernard, A., 2001, Down regulation of melanin concentrating hormone in virally induced obesity: Molecular and Cellular Endocrinology, v. 181, p. 207–219.

Vickers, T., Garcelon, D., Fritcher, D., and Christianson, M., 2004, Evaluation of an oral and food-based canarypox-vectored canine distemper vaccine in endangered Channel Island Foxes (*Urocyon littoralis*): American Association of Zoo Veterinarians, Annual Proceedings, p. 89–90.

Visser, I.K.G., van Bressem, M.F., van de Bildt, M.W.G., Groen, J., Orvell, C., Raga, J.A., and Osterhaus, A.D., 1993, Prevalence of morbilliviruses among pinniped and cetacean species: Reviews in Science and Technology, v. 12, p. 197–202.

Welter, J., Taylor, J., Tartaglia, J., Paoletti, E., and Stephensen, C.B., 1999, Mucosal vaccination with recombinant poxvirus vaccines protects ferrets against symptomatic CDV infection: Vaccine, v. 17, p. 308–318.

Welter, J., Taylor, J., Tartaglia, J., Paoletti, E., and Stephensen, C.B., 2000, Vaccination against canine distemper virus infection in infant ferrets with and without maternal antibody protection, using recombinant attenuated poxvirus vaccines: Journal of Virology, v. 74, p. 6358–6367.

Westover, K.M., and Hughes, A.L., 2001, Molecular evolution of viral F and matrix protein genes and phylogenetic relationships among the Paramyxoviridae: Molecular and Phylogenetic Evolution, v. 21, p. 128–134.

Williams, E., Anderson, S.L., Cavender, J., Lynn, C., List, C., Heran, C., and Appel, M.J.G., 1996, Vaccination of black-footed ferret (*Mustela nigripes*) × Siberian polecat (*M. eversmanni*) hybrids and domestic ferrets (*M. putorius furo*) against canine distemper: Journal of Wildlife Diseases, v. 32, p. 417–423.

Williams, E.S., Edwards, J., Edwards, H., Welch, V., Dubay, S., Luce, B., and Anderson, S., 1997, Survey of coyotes for disease in Shirley Basin, Wyoming in 1996, *in* Luce, B., Oakleaf, B., and Williams, E.S., eds., Black-footed ferret reintroduction, Shirley Basin, Wyoming, 1996 annual completion report: Cheyenne, Wyoming Game and Fish Department, p. 34–43.

Williams, E.S., and Thorne, E.T., 1996, Infectious and parasitic diseases of captive carnivores, with special emphasis on the black-footed ferret (*Mustela nigripes*): Reviews in Science and Technology, v. 15, p. 91–114.

Williams, E.S., Thorne, E.T., Appel, M.J., and Belitsky, D.W., 1988, Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming: Journal of Wildlife Diseases, v. 24, p. 385–398.

Wimsatt, J., Biggins, D., Innes, K., Taylor, B., and Garell, D., 2003, Evaluation of oral and subcutaneous delivery of an experimental canarypox recombinant canine distemper vaccine in the Siberian polecat (*Mustela eversmanni*): Journal of Zoo and Wildlife Medicine, v. 34, p. 25–35.

Wimsatt, J., Jay, M.T., Innes, K.E., Jessen, M., and Collins, J.K., 2001, Serologic evaluation, efficacy, and safety of a commercial modified-live canine distemper vaccine in domestic ferrets: American Journal of Veterinary Research, v. 62, p. 736–740.

Wisely, S.M., Buskirk, S.W., Fleming, M.A., McDonald, D.B., and Ostrander, E.A., 2002, Genetic diversity and fitness in black-footed ferrets before and during a bottleneck: Journal of Heredity, v. 93, p. 231–237.

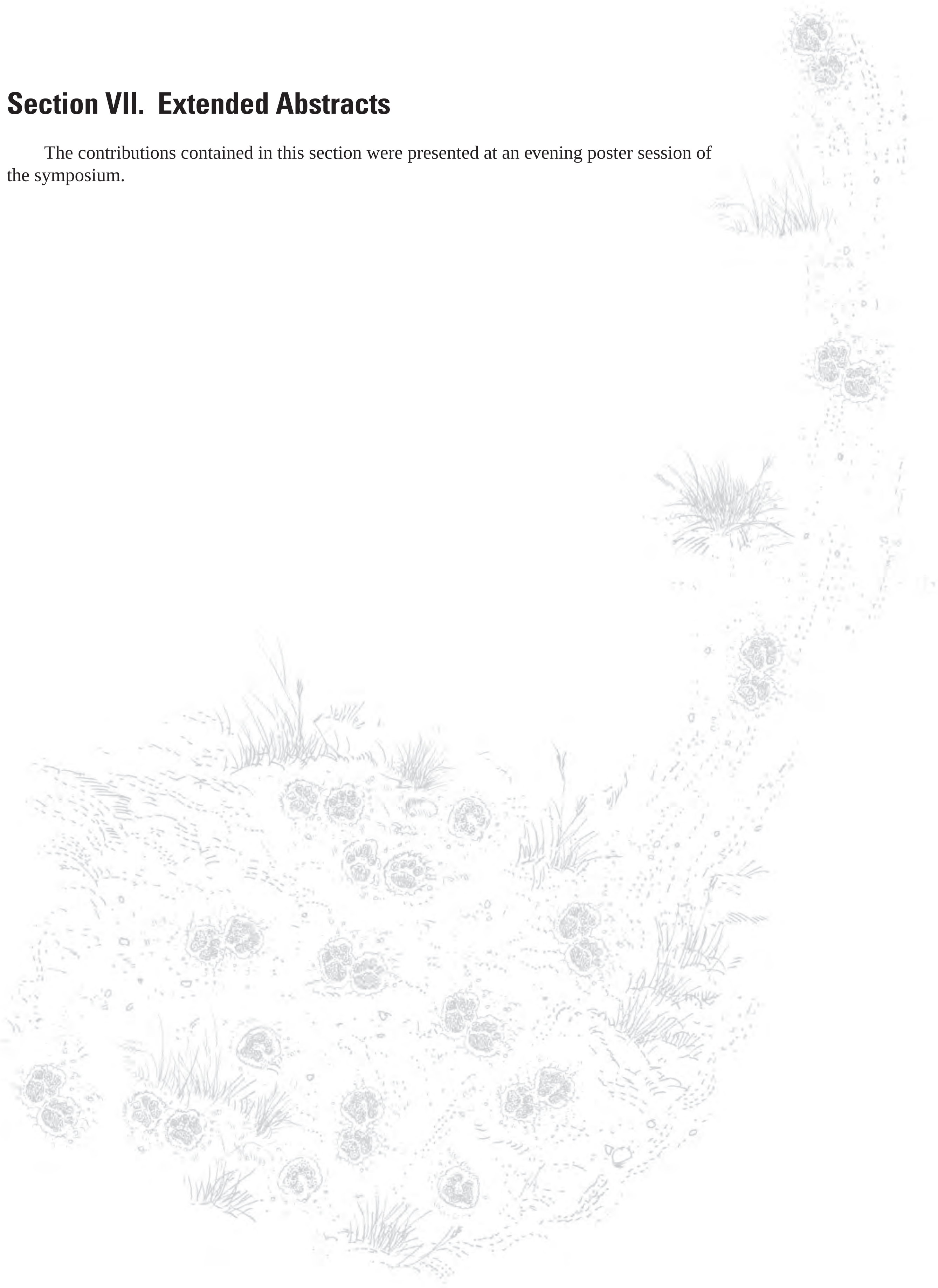
Woolhouse, M.E., Taylor, L.H., and Haydon, D.T., 2001, Population biology of multihost pathogens: Science, v. 292, p. 1109–1112.

Wunschmann, A., Kremmer, E., and Baumgartner, W., 2000., Phenotypical characterization of T and B cell areas in lymphoid tissues of dogs with spontaneous distemper: Veterinary Immunology and Immunopathology, v. 73, p. 83–98.


Heather Bramel
'98

Section VII. Extended Abstracts

The contributions contained in this section were presented at an evening poster session of the symposium.



Identifying Focal Areas for Conservation of Black-footed Ferrets and Prairie Dog Associates

By Jonathan Proctor,[1,2] Bill Haskins,[3] and Steve Forrest[4]

Introduction

Restoring viable populations of black-footed ferrets (*Mustela nigripes*) requires first restoring large complexes of prairie dog (*Cynomys* spp.) colonies. Ferret restoration within the former range of the black-tailed prairie dog (*C. ludovicianus*) requires prairie dog complexes of 4,000 ha or more (Conservation Breeding Specialist Group, 2004). Areas large enough to accommodate prairie dog complexes of this size may not be readily apparent from mapping the current distribution of prairie dogs alone. Remaining prairie dog colony distribution today is in large part an artifact of historical land use rather than habitat suitability or other biotic factors (e.g., Lomolino and Smith, 2003). Moreover, as a result of intensive control efforts, disease, and other management activities, few prairie dog complexes of this size exist in situ today. Necessarily, black-footed ferret recovery will therefore require expansion of prairie dogs into potential habitat, prairie dog translocations, and other "habitat-building" activities. Locating priority opportunities for ferret recovery will involve looking at both biogeographic criteria as well as socioeconomic constraints and concerns. Locating a suite of "restorable" landscapes, based on a coarse set of criteria that account for biological habitat suitability, land tenure, land management, contiguous size, and geographic representation, is a first step in this process (Forrest and others, 2004; Proctor and others, 2006). We used a geographic information system (GIS) to identify areas with restoration potential for the black-footed ferret within the former range of the black-tailed prairie dog, a species for which there are existing models of habitat suitability (e.g., Proctor, 1998).

Methods

We identified potential black-tailed prairie dog habitat within its former range by overlaying a grid of 90 × 90-m pixels on current U.S. Geological Survey vegetation maps (U.S. Geological Survey, 2000). Pixels were considered potential habitat if they contained vegetation classified as grasslands, grassland/herbaceous, shrublands, or transitional areas, removing from consideration all pixels with slopes >10 percent, in cropland, or in the Sandhills region of Nebraska (Proctor and others, 2006).

From this potential prairie dog habitat subset, we selected focal areas for conservation of black-footed ferrets in the following manner. On public lands, we identified as focal areas all contiguous potential prairie dog habitat of 20,000 ha or more. On tribal lands where ownership data were available (Montana and New Mexico), we identified the largest block of potential prairie dog habitat on each reservation with a minimum area of potential habitat >4,000 ha. Where ownership data for tribal lands were unavailable (e.g., the Dakotas and Nebraska), we simply indicated the existence of known large prairie dog complexes (e.g., the Rosebud, Pine Ridge, and Cheyenne River Reservations in South Dakota). We then identified all blocks of potential habitat >4,000 ha located on private reserves (e.g., owned by the Turner Endangered Species Fund or The Nature Conservancy). We placed circles roughly equal to the size of the potential habitat block over the midpoint of each focal area. Circles are meant to identify the general location as opposed to exact boundaries.

The results provided good geographic representation for most states and provinces. However, six States (Kansas, Nebraska, North Dakota, Oklahoma, Texas, Wyoming) contained fewer than five focal areas. In these States, we went below the 20,000-ha cutoff to identify the next largest focal areas on public lands so that each State had at least five focal areas. Finally, because Kansas still had only three focal areas due to limited ownership in public lands or key private lands, we identified an additional two blocks of potential habitat from private lands by iteratively removing the smaller aggregations of potential habitat until only the largest two blocks remained.

In areas where accurate prairie dog location data are available, it may also be possible to develop more robust

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conservation strategies based on “reserve design” concepts (Noss and others, 1999). Using Montana as an example, we identified core conservation areas for prairie dogs and associates, linkage habitat, and matrix habitat by scoring each 90 × 90-m pixel in Montana as follows: 1 if it was classified as potential black-tailed prairie dog habitat, else 0; 1 if it was within a current prairie dog colony (as mapped between 1988 and 2003 and defined by a 0.75-km buffer), else 0; 1 if it was within a block of potential habitat >4,000 ha on public land, tribal land, or a private reserve, else 0; and proximity to other prairie dog colonies, expressed as a value between 0 (at >24 km from a colony) and 1 (on a colony). The final score for each pixel was the total of the individual scores for these four criteria.

Results and Discussion

Using the methodology described, 92 focal areas for potential black-footed ferret recovery were identified (fig. 1). Of the areas identified, five contain seven separate ongoing ferret reintroduction programs; one had ferrets reintroduced, but they no longer survive; and eight have been identified through other processes as having reintroduction potential or are in the process of developing reintroduction programs. Thus, all current or proposed ferret reintroduction sites in the black-tailed prairie dog range were captured by this methodology. While inclusion of all of the current or proposed reintroduction sites provides some validation of the model used here, it also suggests that the most obvious or most readily restorable sites have already been identified and/or are in use. The remaining sites may be progressively more challenging in terms of their restoration potential either because of the lack of currently existing large prairie dog complexes or because of other factors such as resistance to endangered species reintroduction programs.

For Montana, development of a reserve design for ferrets based on multiple attributes is feasible (fig. 2) but also points to limited opportunities for large-scale restoration at multiple sites given current black-tailed prairie dog distribution.

While we limited this analysis to black-tailed prairie dog habitat, data exist to identify black-footed ferret recovery focal areas for both white-tailed (*C. leucurus*) and Gunnison’s (*C. gunnisoni*) prairie dogs as well. Recent assessments of those two species’ ranges suggest that good opportunities may exist in several locations beyond the four sites where recovery activities for ferrets are underway on white-tailed and Gunnison’s prairie dog range (Seglund and others, 2005a,b). A comprehensive, rangewide strategy for ferret recovery should incorporate these and other data to map out a path for the future of the species.

References Cited

Conservation Breeding Specialist Group, 2004, Black-footed ferret population management planning workshop, final report: Apple Valley, Minn., IUCN/SSC Conservation Breeding Specialist Group, 129 p.

Forrest, S.C., Strand, H., Haskins, W.H., Reese, C., Proctor, J., and Dinerstein, E., 2004, Ocean of grass—a conservation assessment for the Northern Great Plains: Bozeman, Mont., Northern Plains Conservation Network and Northern Great Plains Ecoregion Program, World Wildlife Fund–U.S., http://worldwildlife.org/wildplaces/ngp/pubs/ocean-of-grass.cfm.

Lomolino, M.V., and Smith, G.A., 2003, Prairie dog towns as islands—applications of island biogeography and landscape ecology for conserving nonvolant terrestrial vertebrates: Global Ecology and Biogeography, v. 12, p. 275–286.

Noss, R.F., Dinerstein, E., Gilbert, B., Gilpin, M., Miller, G.J., Terborgh, J., and Trombulak, S., 1999, Core areas—where nature begins, *in* Terborgh, J., and Soulé, M., eds., Continental conservation—scientific foundations of regional reserve networks: Washington, D.C., Island Press, p. 99–128.

Proctor, J.D., 1998, A GIS model for identifying potential black-tailed prairie dog habitat in the Northern Great Plains shortgrass prairie: Missoula, University of Montana, M.S. thesis, 54 p.

Proctor, J., Haskins, B., and Forrest, S.C., 2006, Focal areas for conservation of prairie dogs and the grassland ecosystem, *in* Hoogland, J.L., ed., Conservation of the black-tailed prairie dog: Washington, D.C., Island Press, p. 232–247.

Seglund, A.E., Ernst, A.E., Grenier, M., Luce, B., Puchniak, A., and Schnurr, P., 2005a, White-tailed prairie dog conservation assessment: Laramie, Wyo., Western Association of Fish and Wildlife Agencies, 138 p.

Seglund, A.E., Ernst, A.E., and O’Neill, D.M., 2005b, Gunnison’s prairie dog conservation assessment: Laramie, Wyo., Western Association of Fish and Wildlife Agencies, 87 p.

U.S. Geological Survey, 2000, National land cover data: EROS Data Center, Sioux Falls, South Dakota.

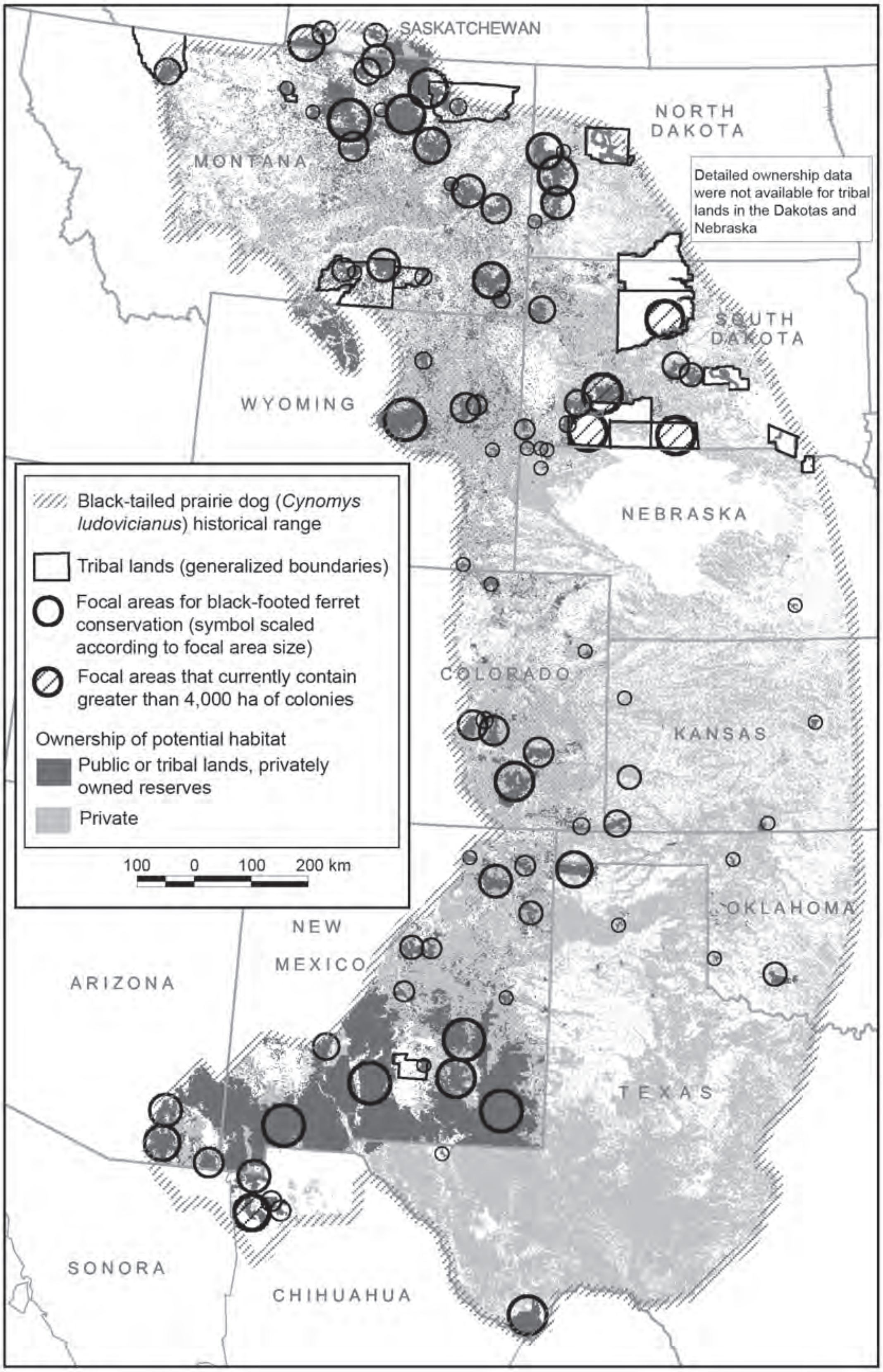

Figure 1. Focal areas for black-footed ferret (*Mustela nigripes*) recovery based on habitat suitability, land tenure, and public land contiguity.

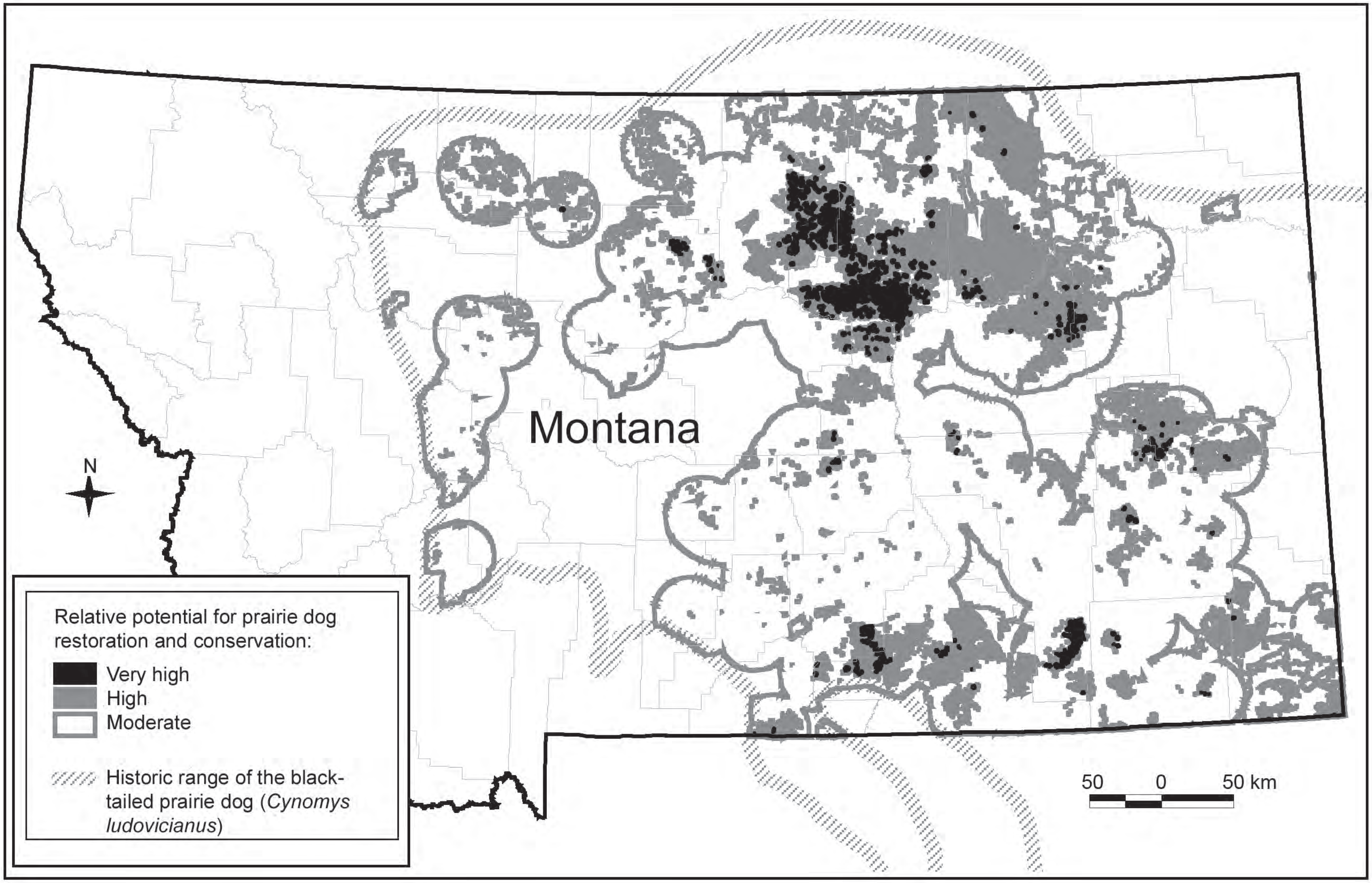

Figure 2. Relative potential for black-footed ferret (*Mustela nigripes*) recovery and restoration in Montana based on scores derived from habitat suitability, land ownership, and existing prairie dog (*Cynomys* spp.) distribution and abundance (moderate score = 1.0–2.0, high = 2.0–3.0, very high = 3.0–4.0).

White-tailed Prairie Dog Population Survey and Habitat Evaluation in Western Wyoming

By John A. Baroch[1,2] and David A. Plume[3]

Introduction

This study was conducted in the Pinedale Anticline Lease Area (PALA) of the Pinedale Field Office administrative unit of the U.S. Bureau of Land Management, Wyoming. The PALA and the adjacent Jonah II Lease Area (J2LA) contain large reserves of natural gas (Lyon and Anderson, 2003) and are sites of rapid energy exploration and extraction activities. The objectives of the study were to assess a variety of demographic variables and to provide a basis for linking prairie dog (*Cynomys* spp.) colonies to land features that might allow modeling of potential habitat. Recently compiled Global Positioning System (GPS) maps of white-tailed prairie dog (*C. leucurus*) colonies within the two mineral leases were available. These maps have been generated and updated annually for several years by a private contractor as part of an ongoing environmental assessment of the mineral leases. Approximately 30 colonies had been identified and mapped within the PALA in 2001. Twenty-nine of these colonies (hereafter referred to as the "base map colonies") were selected to study the demographics and habitat characteristics of white-tailed prairie dogs.

Study Area

The area consists of plains interspersed with isolated hills, plateaus, and low mountains. Elevation ranges from 1,800 to 2,400 m. Winters are cold and summers are short and hot. Average annual precipitation ranges from 130 to 360 mm and is fairly evenly distributed throughout the year. The vegetative community is classified as sagebrush steppe (Reid and others, 2002).

Methods

All burrows on 29 colonies were mapped by GPS in 2003 and classified as active or inactive. Active status was determined by the presence of fresh prairie dog scat in the opening or within 0.5 m of the opening. Fresh scat was defined as greenish, black, or dark brown in color and not dried hard or bleached white (Biggins and others, 1993).

Our survey concentrated on site factors that may influence the selection of white-tailed prairie dog burrows and colonies. Habitat characteristics were compared between the original colonies and nearby "ghost" polygons. The ghost polygons were computer-generated replicas of the actual colonies that were superimposed on the landscape at randomly chosen locations near each actual colony and within a range that was accessible to the prairie dogs (fig. 1).

Soil texture, soil depth, and ground cover were assessed on the colonies surveyed in 2001 and compared with samples from ghost colonies. Soil texture was assessed at a depth of

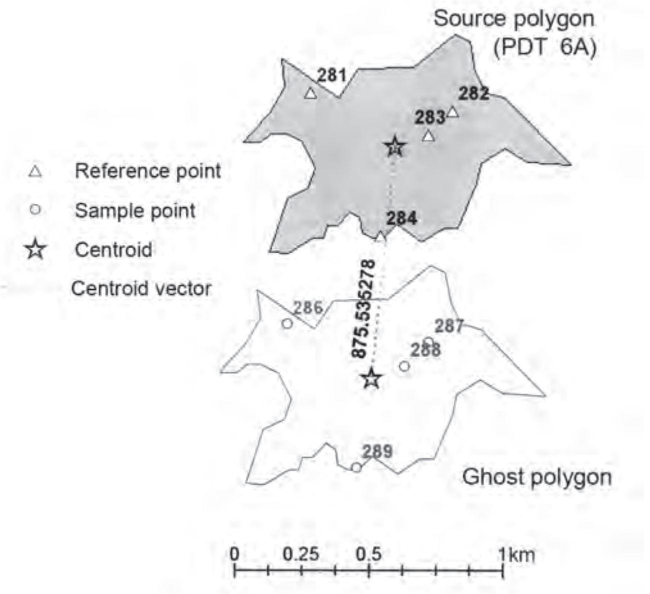

Figure 1. Generating ghost polygons and soil sample sites. Base map white-tailed prairie dog colony (*Cynomys leucurus*) PDT 6A is shown with the corresponding ghost polygon. The four soil survey sites, numbered 281–284, were selected using a randomization procedure applied to numbered cells overlaid on the source polygon. A second randomization algorithm selected the length and direction of the vector connecting the centroids. Soil survey points were projected along the same vector to locate ghost survey points that maintained the geometry of the source polygon.

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0.5 m. Samples were dried and sifted by particle size. Soil depth was defined as the maximum depth (up to 1 m) that could be reached with a hand driven, 8-cm diameter bucket auger. Ground cover and surface soil texture were assessed by the point-intercept survey method. The point-intercept method employs a sighting device or pin/point frame at selected sites to estimate the cover by type. Optical sighting devices eliminate observer bias when used properly since the sampling points are selected entirely by procedure. We fabricated an optical sighting device consisting of a vertical sighting tube with a peephole sight at the top end and an 8-cm diameter glass magnifying lens at the lower end. The sighting tube was attached to the end of a horizontal beam. When rotated 360° in a horizontal plane on a tripod, the optical sight described a circle 1 m in diameter. At each randomly selected sampling location, readings were made at 30° intervals. Cross hairs at the center of the magnifying lens pinpointed each sampling point.

Slope, aspect, and solar gain were derived from 10-m digital elevation model data and intersected with both colony areas and burrow point data. Colony slope and aspect were analyzed with circular statistical methods. The aspect of the 10 × 10-m cell containing each burrow recorded by the GPS was determined, and the results were sorted by active or inactive status.

Results and Discussion

The 2003 survey showed a dramatic reduction in the number of colonies since the earlier survey in 2001, with only 15 of 29 colonies surveyed still active. In terms of area, the active colonies in the vicinity of the 29 original colonies totaled just 71 ha. The original colonies composed 1,407 ha in 2001. Figure 2 illustrates one of the larger colonies that diminished in extent and population between 2001 and 2003. Of the 37 colonies mapped in 2003, 25 had what is considered a favorable or healthy ratio of active to inactive burrows (>1.0) (Biggins and others, 1993). Twelve colonies had ratios below 1.0. The mortality factors that threaten prairie dogs on a large scale include loss of habitat, urbanization, resource development, poisoning, recreational shooting, and sylvatic plague (caused by the bacterium *Yersinia pestis*) (Knowles, 2002). Information on the incidence and impact of plague in the study area is lacking.

Our comparison between the 2001 colonies and the randomly located ghost polygons did not find significant differences in soil depth (to 1 m) or in percent rocks in the soil profile at a depth of 0.5 m. We had hypothesized that variations in soil depth might affect site selection with regard to the ability to establish hibernacula below the frost line. We found soil depth to be at least 1 m throughout the surveyed areas. Since hibernacula are probably always deeper than 1 m, and we were not able to evaluate greater depths, we cannot draw any conclusions as to soil depth being a limiting factor.

The frequency distribution of mineral particle sizes on the surface was found to be almost identical between colonies and ghost polygons. However, there was nearly twice the amount of vegetative cover on colonies as opposed to ghost polygons. The significance of this observation in relation to prairie dog occupancy is unknown.

With respect to slope, aspect, and solar gain, we found that the mean angle and mean vectors were similar for all three sample sets (the base map colonies, ghost polygons, and currently active colonies). Mean angle of all polygons in the three groups was 160° on the base map colonies, 129° among the ghost polygons, and 121° among the currently active colonies. Mean vectors, which express the "evenness" of the dispersion of points around the compass, were 0.556, 0.446 and 0.492, for the base map colonies, ghost polygons, and active colonies, respectively. A value of 1.0 represents uniform dispersion of the vectors on a 360° circle.

The orientation of active and former colonies was found to be exclusively to the northeast, southeast, and southwest quarters of the compass. This orientation avoids the prevailing winds but may also be related to solar flux. Plots of the energy distribution of the entire landscape in the study area, when compared to the energy distribution of active burrow sites, provide evidence that the prairie dogs may be selecting sites within a range of solar gain that differs from expected levels.

We found the slope variation to be very similar in the 2001 colonies and the ghost polygons, but the slope variation on the currently occupied colonies was on average about half that of the other areas. This supports the hypothesis that evenness of slope may facilitate improved communications and predator detection (Wagner, 2002). It is unknown if the prairie

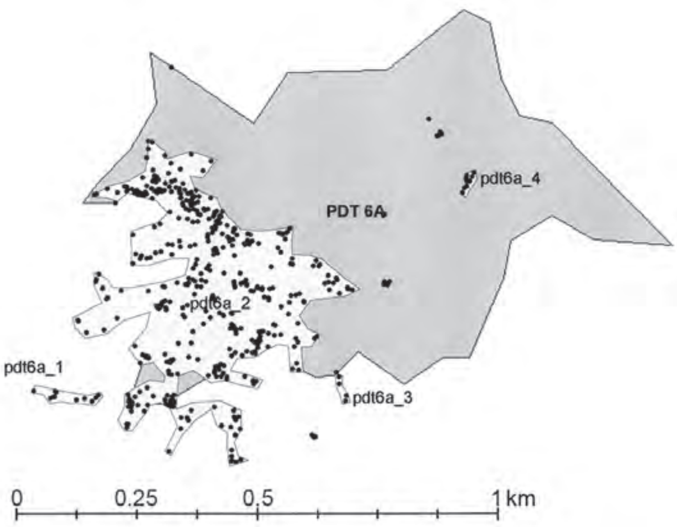

Figure 2. Trend toward fewer active burrows and contracting colony boundaries is illustrated by white-tailed prairie dog (*Cynomys leucurus*) colony PDT 6A. Active burrows recorded by GPS in early summer 2003, overlaid on the colony PDT 6A, mapped in 2001.

dogs preferentially select more even terrain, or if those occupying such terrain are more successful at avoiding predation.

A similar study of the Gunnison's prairie dog (*C. gunnisoni*) in Arizona was used to model habitat associations with the intent that the results might assist managers in estimating the suitability of unoccupied sites for possible prairie dog reintroduction (Wagner 2002). The results of our study may have similar applications for the white-tailed prairie dog.

References Cited

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood., A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Knowles, C., 2002, Status of white-tailed and Gunnison's prairie dogs: Missoula, Mont., National Wildlife Federation, and Washington, D.C., Environmental Defense Fund, 30 p.

Lyon, A.G., and Anderson, S.H., 2003, Potential gas development impacts on sage grouse nest initiation and movement: Wildlife Society Bulletin, v. 31, p. 486–491.

Reid, M., Comer, P., Barrett, H., Caicco, S., Crawford, R., Jean, C., Jones, G., Kagan, J., Karl, M., Kittel, G., Lyon, P., Manning, M., Peterson, E., Rosentreter, R., Rust, S., Tart, D., Williams, C., and Winward, A., 2002, International classification of ecological communities—terrestrial vegetation of the United States. Sagebrush vegetation of the Western United States: Arlington, Va., NatureServe, Final report for the U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Boise, Idaho, 23 p.

Wagner, D.M., 2002, Current status and habitat use of Gunnison's prairie dogs (*Cynomys gunnisoni*) in Arizona: Flagstaff, Northern Arizona University, Ph.D. dissertation, 77 p.

Can the Systemic Insecticide Nitenpyram Be Used for Flea Control on Black-tailed Prairie Dogs?

By Jeff N. Borchert[1] and Jeff J. Mach[1]

Introduction

Plague has the potential to decimate prairie dog (*Cynomys* spp.) populations and is a threat to reintroduction of the black-footed ferret (*Mustela nigripes*), which requires large colonies of prairie dogs for food (Biggins and Godbey, 2003). Controlling flea (Insecta: Siphonaptera) populations on prairie dogs at reintroduction sites could decrease the risk of plague. Currently, fleas in prairie dog towns are controlled by using permethrin or deltamethrin dust (Beard and others, 1992; Seery, 2003). However, these compounds may be detrimental to nontarget arthropods.

Systemic insecticides, commonly used for flea control in veterinary medicine, might be useful in controlling flea populations on prairie dogs, but little use has been made of such compounds added to rodent bait for control of plague (Gratz, 1999). Nitenpyram is an insecticide that has been used for the control of aphids, thrips, leafhoppers, whiteflies, and other suckling insects of rice and has also demonstrated effectiveness against the cat flea (*Ctenocephalides felis*) as a topical treatment (Tomlin, 2000; Moyses and Gfeller, 2001). Nitenpyram is also effective for systemic control of fleas on pets and is currently used in a commercial systemic flea treatment for dogs and cats called Capstar® (Novartis Animal Health, Greensboro, N.C.) (Rust and others, 2003). We investigated the efficacy of systemically delivered nitenpyram formulated at 560 mg/kg in rodent bait against a ground squirrel flea (*Oropsylla montana),* which readily transmits plague, on black-tailed prairie dogs (*C. ludovicianus*).

Methods

Prairie dogs were captured in Larimer County, Colo., transported to Genesis Laboratories, Inc., and acclimated to laboratory conditions for 13 days. Medicated prairie dog bait was prepared by mixing 20 Capstar tablets (56 mg nitenpyram/tablet) in palatable grains and powdered sugar (2 kg total). The medicated diet was presented to the prairie dogs for 48 hours. Food consumption was measured daily. Artificial flea feeding apparatuses were constructed with centrifuge tubes, 300 µm nylon mesh, and plumber's glue to allow fleas to feed without being lost. Four to six fleas (*O. montana*) obtained from the Genesis Laboratories breeding colony were added to each flea feeder. The apparatuses were secured to prairie dogs for 24 hours with athletic tape on an area of shaved fur. The apparatuses were then removed, and the fleas were immediately evaluated for mortality and morbidity by placing them in a large white plastic container. By blowing on the fleas, we could ascertain mortality or morbidity by the presence or absence of movement. The process was repeated on day 3 after exposure for evaluation of residual effect.

Results

Bait containing 560 mg/kg nitenpyram was effective at producing mortality and morbidity in fleas at day 1 (table 1) and minimally at day 3. Day 1 flea mortality was 76.9 percent. Of the 11 fleas surviving, 5 (45.5 percent) were observed to be moribund. Day 3 flea mortality was 23.1 percent. Of the 10 fleas surviving at day 3, 0 (0 percent) were observed to be moribund.

Discussion and Management Implications

Nitenpyram was initially effective at controlling *O. montana* fleas on black-tailed prairie dogs, causing greater than 70 percent mortality at day 1. Mortality of fleas declined to 23.1 percent by day 3. Observations in other ground squirrels (*Spermophilus* spp.) indicate that recolonization of hosts by fleas is very rapid, within 3 days (Ryckman, 1971). Because of the lack of residual action of systemically delivered nitenpyram, this compound would likely not be effective as a method of preventative plague control in prairie dogs. A systemically delivered insecticide with longer residual effect might be beneficial in a plague control program of this type.

In addition to their potential utility in controlling fleas on prairie dogs at black-footed ferret recovery sites, rodent baits containing insecticide might also be effective for preventative flea control in situations where rodents live close to humans,

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Table 1. The 24-hour efficacy of systemic nitenpyram on *Oropsylla montana* fed on black-tailed prairie dogs (*Cynomys ludovicianus*).

Prairie dog number	Sex	Active ingredient consumed (mg)	Body weight (kg)	Dose (mg/kg)	Number of fleas applied	Fleas dead/ fleas recovered	Fleas moribund/ fleas recovered alive
				Treatment			
1	M	25.9	0.827	31.3	5	Not recovered	
3	M	35.3	0.475	74.3	4	3/4	0/1
4	F	4.0	0.798	5.0	4	1/4	1/3
6	M	29.3	0.924	31.7	5	5/5	-
7	M	12.4	0.895	13.9	5	5/5	-
8	M	21.8	1.109	19.7	5	4/5	1/1
9	M	38.9	1.175	33.1	6	6/6	-
11	F	2.3	0.710	3.2	5	2/5	0/3
12	M	42.0	1.111	37.8	5	5/5	-
14	F	24.7	0.773	32.0	4	2/4	1/1
15	M	23.4	1.225	19.1	4	3/4	1/1
16	F	27.9	0.964	28.9	5	4/5	1/1
Mean		24.0	0.916	27.5	Total	40/52 (76.9%)	5/11 (45.5%)
				Control			
1	M	-	0.775	-	4	0/4	-
2	M	-	1.159	-	5	0/5	-
3	M	-	0.655	-	5	1/5	-
4	M	-	0.872	-	5	0/5	-
Mean		-	0.865	-	Total	1/19 (5.3%)	-

but other rodent control methods are not acceptable to the public. For example, the City of Fort Collins, Colo., maintains approximately 2,000 acres of active black-tailed prairie dog colonies within the Urban Growth Area. Lethal control of these prairie dogs has been a contentious issue among Fort Collins residents (City of Fort Collins, 1998). Baits incorporating insecticides might be ideal in such a situation as potential risk to humans would likely decrease and the prairie dogs themselves would not be harmed.

References Cited

Beard, M.L., Rose, S.T., Barnes, A.M., and Montenieri, J.A., 1992, Control of *Oropsylla hirsute*, a plague vector, by treatment of prairie dog burrows with 0.5% permethrin dust: Journal of Medical Entomology, v. 29, p. 25–29.

Biggins, D.E., and Godbey, J.L., 2003, Challenges to reestablishment of free-ranging populations of black-footed ferrets: Comptes Rendus Biologies, v. 326 (Suppl. 1), p. S104–S111.

City of Fort Collins, 1998, Prairie dog policies for natural areas: Fort Collins, Colo., Prairie Dog Review Committee, Natural Resources Department, 24 p.

Gratz, N.G., 1999, Control of plague transmission, *in* Plague manual: Geneva, Switzerland, World Health Organization, p. 97–134.

Moyses, E.W., and Gfeller, F.J., 2001, Topical application as a method for comparing the effectiveness of insecticides against cat flea (Siphonaptera: Pulicidae): Journal of Medical Entomology, v. 38, p. 193–196.

Rust, M.K., Waggoner, M.M., Hinkle, N.C., Stansfield, D., and Barnett, S., 2003, Efficacy and longevity of nitenpyram against adult cat fleas (Siphonaptera: Pulicidae): Journal of Medical Entomology, v. 40, p. 678–681.

Ryckman, R.E., 1971, Plague vector studies 3. The rate deparasitized ground squirrels are reinfested with fleas under field conditions: Journal of Medical Entomology, v. 8, p. 668–670.

Seery, D.B., Biggins, D.E., Montenieri, J.A., Enscore, R.E., Tanda, D.T., and Gage, K.L., 2003, Treatment of black-tailed prairie dog burrows with deltamethrin to control fleas (Insecta: Siphonaptera) and plague: Journal of Medical Entomology, v. 40, p. 718–722.

Tomlin, C.D.S., 2000, The pesticide manual: Farnham, U.K., British Crop Protection Council, 1,344 p.

Fleas and Small Mammal Hosts Within and Adjacent to the Coyote Basin White-tailed Prairie Dog Colony in Northeastern Utah

By Lianna K. Etchberger,[1] William E. Stroh,[2] Brent D. Bibles,[3] Matthew R. Dzialak,[1] and Richard C. Etchberger[1]

Introduction

The endangered black-footed ferret (*Mustela nigripes*) and its prairie dog (*Cynomys* spp.) prey are susceptible to sylvatic plague, an infectious disease caused by the bacterium *Yersinia pestis*. Plague is a contagious disease transmitted by bites of vector fleas (Insecta: Siphonaptera), consumption of infected tissue, or contact with infected animals. Epizootics of plague are a threat to prairie dog and ferret populations at most reintroduction sites due to high mortality rates of both ferrets and prairie dogs. While much effort is currently focused on protecting these species from plague by flea control and vaccine development, little is understood about the reservoirs of this disease in the wild. Contributions to this understanding will lend insight for designing plague monitoring and transmission prevention protocols and for any effort to expand habitat for black-footed ferrets and prairie dogs.

Factors influencing the occurrence of plague epizootics are not fully understood (reviewed in Gage and Kosoy, 2005). In the arid Southwest, for example, favorable climate conditions correlate with plague epizootics (Parmenter and others, 1999; Enscore, 2002). While other models exist, there is speculation that climate may correlate with epizootics through increased rodent host populations (Parmenter and others, 1999; Enscore and others, 2002; Stapp and others, 2004). High population density increases the likelihood of transmission of a contagious disease once the pathogen is introduced to the susceptible population (Madigan and others, 2000). Population growth can also lead to expansion into adjacent areas atypical of short grassland prairie dog habitat. Indeed, active and inactive burrows have been found in dense sagebrush and on hillsides in a white-tailed prairie dog (*C. leucurus*) colony in Coyote Basin in northeastern Utah (L. Etchberger, personal observation, 1999). White-tailed prairie dog expansion into new habitat may therefore result in increased exposure to one or more flea or small mammal host species that are more likely to transmit plague to the population. This increased exposure may be caused by either overlapping ranges between the prairie dogs and flea vector or reservoir host or by expansion into an area with increased frequency of either the vector or the reservoir. While different flea species have different biological transmission rates in laboratory settings, mechanical transmission has also been observed (reviewed in Gage and Kosoy, 2005), suggesting that most flea species may be potential candidates for transmission in the wild. In this study, we present preliminary analyses of data comparing small mammal hosts and their flea species collected from white-tailed prairie dog habitat to those collected from adjacent habitat with the potential for prairie dog expansion. Patterns of flea species associations with host or habitat may help identify potential plague reservoirs.

Methods

We used field data on prairie dog distribution in Coyote Basin, Utah, and a geographic information system (ArcView®; Environmental Systems Research Institute, Inc., Redlands, Calif.) to delineate habitat occupied by white-tailed prairie dogs (PD) and adjacent habitat that was not occupied by prairie dogs (NOPD). Occupied habitat included a 50-m buffer adjacent to the colony perimeter; all habitat delineated as NOPD was at least 50 m from the colony boundary. We established small mammal trapping grids within PD and NOPD areas. To select specific grid locations, we used ArcView to generate 20 random points in each area, and we surveyed these locations systematically. Upon identifying a location in each area that we considered appropriate logistically, we selected that location as the southwest corner of a trapping grid. Grids consisted of 100 Sherman live traps placed 10 m apart in a 10 × 10 array. Grids were revisited for two to four trapping

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sessions each summer. Small mammals were trapped for two consecutive nights on the four grids (800 trap nights) during each session. Animals trapped on the second night were processed by determining weight and sex and combing for fleas after anesthesia with isoflurane. We restricted processing to animals trapped on the second night to facilitate objectives of additional research not presented here. Fleas were collected in a tube with saline/Tween detergent solution, pooled for each individual host animal, and sent to the Bacterial Zoonoses Branch, Centers for Disease Control and Prevention (CDC) in Fort Collins, Colo., for species identification. We used Fisher's exact test to evaluate differences in the occurrence of small mammal species, flea species, or flea host species distributed between PD and NOPD habitats. Significance was set at $P \leq 0.05$.

Results

A preliminary analysis of pooled data collected between the years 2000 and 2004 is reported here. Spatial and temporal analyses will be reported elsewhere.

Small mammal species and their distribution between the PD and NOPD locations are shown in table 1. The majority (96 percent) of small mammals trapped were deer mice (*Peromyscus maniculatus*). We also trapped Ord's kangaroo rats (*Dipodomys ordii*) and piñon mice (*P. truei*) along with one northern grasshopper mouse (*Onychomys leucogaster*) and one thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). Of the 822 small mammals trapped, 405 were trapped in PD grids and 417 were trapped in NOPD grids. Differences in the occurrence of small mammal species between PD and NOPD habitats were significant ($P = 0.04$), largely reflecting the differences in abundance of Ord's kangaroo rats between sites.

Table 1. Distribution of small mammals and fleas from habitats occupied (PD) and not occupied (NOPD) by white-tailed prairie dogs (*Cynomys leucurus*).

	PD	NOPD	Species total
Small mammals			
Deer mouse (*Peromyscus maniculatus*)	396	396	792
Ord's kangaroo rat (*Dipodomys ordii*)	5	17	22
Piñon mouse (*P. truei*)	3	3	6
Northern grasshopper mouse (*Onychomys leucogaster*)	1	0	1
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	0	1	1
Total	405	417	822
Fleas			
Aetheca wagneri	136	122	258
Meringus sp.	2	17	19
Epitidea wemmani	2	10	12
Amaradix euphorbi	5	3	8
Orchopeas sexdentatus	0	2	2
Total	145	154	299

Flea species and their distribution between the PD and NOPD locations are shown in table 1. The majority (86 percent) of fleas collected were *Aetheca wagneri*; *Meringus* sp., *Epitidea wemmani*, *Amaradix euphorbi*, and *Orchopeas sexdentatus* were also collected. There was some concern at the CDC as to whether the *O. sexdentatus* identification was correct because this species is not normally associated with the deer mouse host on which it was found. Of the 299 fleas collected, 145 were collected from small mammal hosts trapped in PD grids, and 154 were from NOPD grids. The difference in the occurrence of flea species between PD and NOPD habitats was significant ($P < 0.01$), reflecting the increased occurrence of *Meringus* sp. and *E. wemmani* in NOPD locations.

All fleas collected were from deer mice and Ord's kangaroo rats. The flea/host relationships and distributions are shown in table 2. Numbers represent host species infested with each flea species. The majority of infested hosts were deer mice with *A. wagneri* fleas. There was no statistical difference in the flea/host relationships between the PD and NOPD habitats; the occurrence of deer mice, Ord's kangaroo rats, and total number of hosts infested with various flea species did not vary between the two habitats ($P = 0.27$, 0.29, and 0.44, respectively).

Discussion

Small mammals and their fleas were collected in the white-tailed prairie dog colony of Coyote Basin, Utah, for the

Table 2. Numbers of small mammals infested with fleas from habitats occupied (PD) and not occupied (NOPD) by white-tailed prairie dogs (*Cynomys leucurus*).

	Deer mouse (*Peromyscus maniculatus*)			Ord's kangaroo rat (*Dipodomys ordii*)		
	PD	NOPD	Total	PD	NOPD	Total
Aetheca wagneri	70	63	133	1	0	1
Meringus sp.	1	1	2	1	5	6
Epitidea wemmani	2	7	9	0	0	0
Amaradix euphorbi	2	1	3	0	0	0
Orchopeas sexdentatus	0	1	1	0	0	0
Total infested hosts	75	73	148	2	5	7

past five seasons. By returning to the same grid locations every year in this ongoing study, we have boosted our small sample sizes to better detect patterns in species composition and abundance. By comparison to prairie dog-occupied habitat, we observed that Ord's kangaroo rats and *E. wemmani* and *Meringus* sp. fleas were more abundant outside the colony boundary. Whereas deer mice were equally distributed, those infested with *E. wemmani* occurred more often in habitat outside of the colony. Also, *Meringus* sp. was found on both deer mice and Ord's kangaroo rats, an interesting observation since many flea species associate with only one host species. The preliminary observation that these flea and host species occur more frequently outside but near the Coyote Basin white-tailed prairie dog colony may have implications in plague transmission to prairie dogs and black-footed ferrets from an unidentified reservoir.

References Cited

Enscore, R.E., Biggerstaff, B.J., Brown, T.L., Fulgham, R.F., Reynolds, P.J., Engelthaler, D.M., Levy, C.E., Parmenter, R.R., Montenieri, J.A., Cheek, J.E., Grinnell, R.K., Ettestad, P.J., and Gage, K.L., 2002, Modeling relationships between climate and the frequency of human plague cases in the southwestern United States, 1960–1997: American Journal of Tropical Medicine and Hygiene, v. 66, p. 186–196.

Gage, K.L., and Kosoy, M.Y., 2005, Natural history of plague—perspectives from more than a century of research: Annual Review of Entomology, v. 50, p. 505–528.

Madigan, M.T., Martinko, J.M., and Parker, J., 2000, Brock biology of microorganisms (9th ed.): Upper Saddle River, N.J., Prentice-Hall, Inc., 991 p.

Parmenter, R.R., Yadav, E.P., Parmenter, C.A., Ettestad, P., and Gage, K.L., 1999, Incidence of plague associated with increased winter-spring precipitation in New Mexico: American Journal of Tropical Medicine and Hygiene, v. 61, p. 814–821.

Stapp, P., Antolin, M.F., and Ball, M., 2004, Patterns of extinction in prairie dog metapopulations—plague outbreaks follow El Niño events: Frontiers in Ecology and the Environment, v. 2, p. 235–240.

Effects of Moonlight on Cover Usage and Spatial Learning of Black-footed Ferrets

By Samantha N. Marcum,[1,2] Dean E. Biggins,[3] and Jennifer A. Clarke[1]

Conservation biology and animal behavior are two fields of science that can complement one another. Animal behavior research is important for understanding the complex needs of a species to be managed or restored to its native range and can be a critical part of the foundation for preservation of a species. Black-footed ferrets (*Mustela nigripes*) are endangered, nocturnal carnivores native to the North American prairie ecosystem. Siberian polecats (*M. eversmannii*) are their closest living relative and inhabit the steppe grasslands of Asia and Eastern Europe. Polecats were used as a surrogate species for behavioral studies in the initial stages of restoration attempts for the black-footed ferret. In previous studies, ferrets and polecats were highly susceptible to predation (Biggins, 2000). In this study, we hypothesized that ferrets and polecats would react to moonlight similarly to small nocturnal mammalian prey species that decrease activity and increase use of cover with increasing moonlight to avoid predation (Kavanau, 1969; Clarke, 1983; Falkenberg and Clarke, 1998; Zollner and Lima, 1999). We investigated the effects of moonlight on nocturnal cover usage and spatial learning abilities of black-footed ferrets. Multivariate general linear models with a repeated measures design were used to analyze data with $P = 0.05$ chosen as the significance level.

We tested cover usage by black-footed ferrets ($n = 8$) in an indoor chamber (7 m^2) under simulated new (0.05 lux), half (0.35 lux), and full (2.2 lux) moonlight levels. We measured use of cover (edge, burrows) and open areas. We detected no effect of moonlight level on use of cover versus open space for black-footed ferrets. Free-ranging ferrets and polecats studied previously increased their aboveground activity and movements with increasing moonlight levels, and black-footed ferret activity was low during primary activity periods of their principal predators, regardless of moonlight levels (Biggins, 2000). Energetic demands of ferrets may not allow moonlight to be a principal determinant of activity even if they prefer certain light levels. Also, light may be beneficial for spatial learning of home ranges, finding burrows, and locating prey or mates.

Spatial learning refers to the ability to remember the location of key features in one's environment (Gaulin and Fitzgerald, 1989; Lavenex and Schenk, 1998). Ferrets may use moonlight to examine their surroundings. We tested black-footed ferret spatial learning abilities (as indexed by distance traveled before the subject found a goal in a faux burrow) in a hexagonal indoor chamber (9 m^2) in new, half, and full moonlight levels. The ferrets typically stayed close to the walls of the arena during trials, a behavior known as thigmotaxy. Black-footed ferrets seemed to learn, but moonlight levels appeared to have no effect on that process. Polecats tested in another study that used similar methods (Sheffer, 2001) exhibited spatial learning abilities that appeared to be enhanced in half moonlight. Black-footed ferrets may be more nocturnally adapted than polecats (Biggins, 2000; Sheffer, 2001). Both species traveled less with successive spatial learning trials, suggesting that they either learned the goal location or the ritual for the test (fig. 1). Black-footed ferrets did not decrease the distance traveled to locate the goal in full moonlight; there was no evidence for a positive correlation between spatial learning and light level. Overall, black-footed ferrets traveled shorter distances than did polecats (fig. 1). Learning abilities of both species should be examined further to determine how cage rearing might affect spatial learning skills (e.g., Biggins and others, 1998). If these skills can be lost or fail

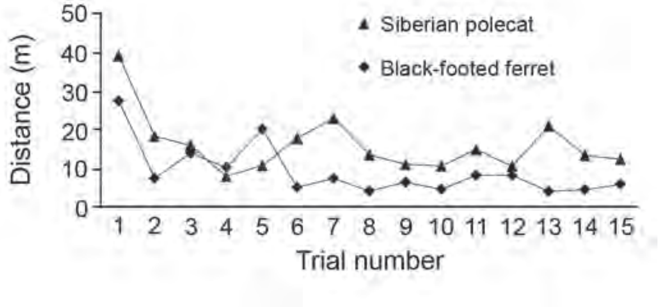

Figure 1. Mean distance traveled (m) by black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*) during 15 consecutive trials.

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to develop without appropriate stimuli, then modifications in captive breeding facilities may be necessary. Understanding these aspects of ferret behavior may be critical to conservation efforts for the species, particularly the success of captive breeding programs and species restoration. For example, better understanding of ferret behaviors under varying light levels may lead to increased efficiency in searching for ferrets (Biggins, Godbey, Matchett, and others, this volume) and improved interpretations of both energetic relationships (Harrington and others, this volume) and interactions with other predators (Breck and others, this volume).

References Cited

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 185 p.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Clarke, J.A., 1983, Moonlight's influence of predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*): Behavioral Ecology and Sociobiology, v. 13, p. 205–209.

Falkenberg, J.C., and Clarke, J.A., 1998, Microhabitat use of deer mice: effects of inter-specific interaction risks*:* Journal of Mammalogy, v. 79, p. 558–565.

Gaulin, S., and Fitzgerald, R., 1989, Sexual selection for spatial-learning ability: Animal Behaviour, v. 37, p. 322–331.

Kavanau, J.L., 1969, Influences of light on activity of small mammals: Ecology, v. 50, p. 548–557.

Lavenex, P., and Schenk, F., 1998, Olfactory traces and spatial learning in rats: Animal Behaviour, v. 56, p. 1129–1136.

Sheffer, K.H., 2001, The effect of moonlight on spatial learning in steppe ferrets: Greeley, University of Northern Colorado, M.S. thesis, 48 p.

Zollner, P.A., and Lima, S.L., 1999, Illumination and the perception of remote habitat patches by white-footed mice: Animal Behaviour, v. 58, p. 489–500.

Modeling Black-footed Ferret Energetics: Are Southern Release Sites Better?

By Lauren A. Harrington,[1,2] Dean E. Biggins,[3] and A. William Alldredge[1]

Introduction

Several models have been developed to estimate prey requirements and to assess habitat suitability of release sites for the black-footed ferret (*Mustela nigripes*) (e.g., Stromberg and others, 1983; Powell and others, 1985; Biggins and others, 1993). None of these models, however, addressed possible differences in energetic requirements between sites due to climatic differences within the ferret's historical range. We used a simplified energetics model to examine the effect of variation in environmental conditions on ferret energetic requirements. The aim of the study was to determine whether the ferret might be more successful in one area than another.

The Model

The total daily energy expenditure (E_{DEE}) of any mammal can be conceptualized as the sum of all mutually exclusive sources of energy expenditure (E_x) (Wunder, 1975; Powell and others, 1985). For a nonreproductive, fully grown adult, E_{DEE} can be modeled in the general form:

$$E_{DEE} = E_s + E_a + E_t$$

where E_s is the energy cost of resting; E_a is the energy cost of activity, including, in this case, running (E_r), digging (E_d), and standing (E_{st}) (Powell and others, 1985); and E_t is the energy cost of thermoregulation. We included thermoregulatory costs below the animal's lower critical temperature (T_{LC}) only and divided this into the cost above ground (E_{ta}) and below ground (E_{tu}). The inclusion of thermoregulation in the model was conditional upon Ta input. We estimated the total energy requirements of the animal for one day (in kJ) as:

$$E_{DEE} = E_s + E_r + E_d + E_{st} + [\text{if } Ta_a < T_{LC}]\ E_{ta} + [\text{if } Ta_u < T_{LC}]\ E_{tu}$$

where E_i is estimated as $M_i \times t_i$ (M_i is the energetic cost of activity i in kJ per hour; t_i is the time spent in activity i in hours per day), Ta_a is the ambient temperature above ground, and Ta_u is the temperature within the burrow (details in Harrington, 2001).

Model parameter estimates were from the literature, with empirical data on black-footed ferret metabolism from Harrington (2001) and Harrington and others (2003) and site temperature data (Ta_a) from meteorological records.

Model Simulations

For three hypothetical sites in the extreme north, south, and middle of the ferret's historical range, the model was run for 11 different activity scenarios ranging from complete rest within burrows to 5 hours active above ground (activity data from Powell and others, 1985). For each model run, Ta_a was chosen at random from a hypothesized normal distribution approximating nighttime temperature for each site in summer and winter. Ta_u was chosen at random from a range of values from the literature for summer and winter (same for all sites). Means and variances were based on 100 runs of the model for each of the 11 activity scenarios, for each site, in winter and summer.

Results

Assuming all activity scenarios are carried out at all sites in winter and summer, the model predicted higher energy requirements in the north than in the south in winter. In summer, energy requirements were predicted to be lower in the south than in the middle of the ferret's range. All other comparisons were nonsignificant. In all cases, variability within a site and season was high due to the inclusion of all possible activity scenarios in the simulations. Separating the analysis into low, medium, and high activity levels revealed that although trends tended to be similar (higher in the north than in the south), differences between sites were greatest at high activity levels and during winter. For resting ferrets, no differences between sites were detected; this was, however, an artifact of the model resulting from the use of a constant value

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for Ta_u. If burrow temperatures do vary between sites, overall intersite differences are likely to be greater.

Discussion

Although our model predicted statistically significant differences in energy requirements between northern and southern sites, these differences were small (<100 kJ per day between sites or about 11 percent of total mean expenditure during winter) and would require only small increases in prey consumption (one black-tailed prairie dog [*Cynomys ludovicianus*], the ferret's main prey, provides between 4,000 and 5,000 metabolizable kJ of energy; Powell and others, 1985). More biologically meaningful differences were found in consideration of energetic limits.

If maximum sustained metabolic rates for ferrets are limited at five times the basal metabolic rate (as they are for most other animals; Hammond and Diamond, 1997), maximum daily energy expenditure may be limited to approximately 1200 kJ per day, or less. Plotting predicted energy required per day in relation to above ground temperature demonstrated that, on this basis, high activity levels may be prohibitive at temperatures below -35°C (fig. 1). Although ferrets have been observed above ground at temperatures as low as -40°C (Richardson and others, 1987), it is not known how long they can stay above ground at such extremes. Ferret movements are shorter in colder temperatures; on the coldest days, ferrets simply may not be able to remain above ground. Ferret movements in late winter are principally for mating (Richardson and others, 1987); thus, restricted activity at this time could adversely affect reproductive potential.

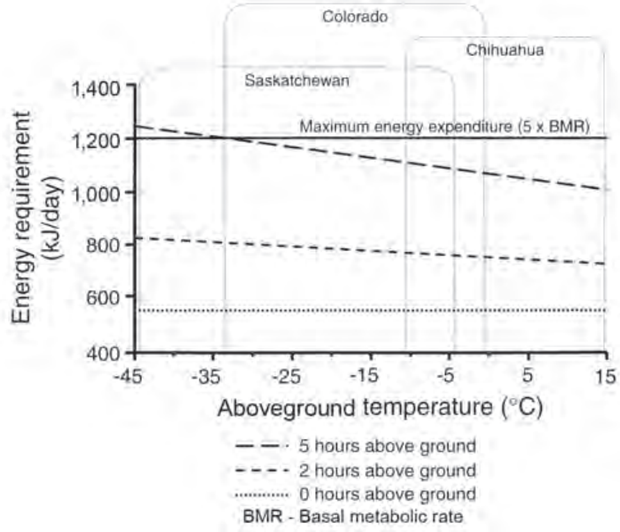

Figure 1. Predicted daily energy requirements for a black-footed ferret (*Mustela nigripes*) in winter in relation to aboveground temperature and amount of time spent above ground. Bracketing lines depict the range of winter temperatures for example sites. Activity was modeled to include mostly running with some time spent standing; Ta_u was set at 7.5°C (midpoint of the winter range).

Management Implications and Questions Remaining

This study does not provide definitive answers regarding the effect of climatic variability on ferret energy requirements. It does suggest, however, that ferret energetics and climate may be important factors to consider in evaluating potential release sites. If ferrets are to be successfully reintroduced into the wild, management plans should seek to minimize sources of stress to the extent possible. Winter energy requirements may be reduced by selecting more southerly reintroduction sites. As with all models, our predictions will require field validation. Questions remaining include (but are not limited to) the following. Is water stress greater in the south? How much do burrow temperatures vary between sites (and can ferrets manipulate their own burrow temperature by selecting depth)? How does ferret activity vary throughout their range (and in response to climate)?

References Cited

Biggins, D.E., Miller, B.J., Hanebury, L.R., Oakleaf, B., Farmer, A.H., Crete, R., and Dood, A., 1993, A technique for evaluating black-footed ferret habitat, *in* Oldemeyer, J.L., Biggins, D.E., Miller, B.J., and Crete, R., eds., Management of prairie dog complexes for the reintroduction of the black-footed ferret: Washington, D.C., U.S. Fish and Wildlife Service, Biological Report 13, p. 73–88.

Hammond, K.A., and Diamond, J., 1997, Maximal sustained energy budgets in humans and animals: Nature, v. 386, p. 457–462.

Harrington, L.A., 2001, Application of an energetics model to evaluate release-site potential for the black-footed ferret (*Mustela nigripes*): Fort Collins, Colorado State University, M.S. thesis, 126 p.

Harrington, L.A., Biggins, D.E., and Alldredge, A.W., 2003, Basal metabolism of the black-footed ferret (*Mustela nigripes*) and the Siberian polecat (*M. eversmannii*): Journal of Mammalogy, v. 84, p. 497–504.

Powell, R.A., Clark, T.W., Richardson, L., and Forrest, S.C., 1985, Black-footed ferret *Mustela nigripes* energy expenditure and prey requirements: Biological Conservation, v. 34, p. 1–15.

Richardson, L., Clark, T.W., Forrest, S.C., and Campbell, T.M., III, 1987, Winter ecology of black-footed ferrets

(*Mustela nigripes*) at Meeteetse, Wyoming: American Midland Naturalist, v. 117, p. 225–239.

Stromberg, M.R., Rayburn, R.L., and Clark, T.W., 1983, Black-footed ferret prey requirements—an energy balance estimate: Journal of Wildlife Management, v. 47, p. 67–73.

Wunder, B., 1975, A model for estimating metabolic rate of active or resting mammals: Journal of Theoretical Biology, v. 49, p. 345–354.

Roelle and others, eds.—**Recovery of the Black-footed Ferret: Progress and Continuing Challenges**—U.S. Geological Survey Scientific Investigations Report 2005-5293

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Perspective

Conservation's blind spot: The case for conflict transformation in wildlife conservation

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ABSTRACT

Unaddressed or poorly addressed conflicts present increasingly difficult obstacles to effective conservation and management of many wildlife species around the world. The material, visible manifestations of such conflicts are often rooted in less visible, more complex social conflicts between people and groups. Current efforts to incorporate stakeholder engagement typically do not fully acknowledge or address the social conflicts that lie beneath the surface of conservation issues, nor do they consistently create the necessary conditions for productive transformation of the root causes of conflict. Yet, the ultimate level of social carrying capacity for many species will depend on the extent to which conservation can reconcile these social conflicts, thereby increasing social receptivity to conservation goals. To this end, conservation conflict transformation (CCT) offers a new perspective on, and approach to, how conservationists identify, understand, prevent, and reconcile conflict. Principles and processes from the peacebuilding field inform CCT and offer useful guidance for revealing and addressing social conflicts to improve the effectiveness of conservation efforts. The Human-Wildlife Conflict Collaboration (HWCC) has adapted and demonstrated these principles for application in conservation through capacity building and conflict interventions, transforming how many practitioners in the conservation field address conflict. In this article, we discuss current limitations of practice when addressing conflict in conservation, define conflict transformation, illustrate two analytical models to orient the reader to the benefits of CCT, and present two case studies where CCT was applied usefully to a conservation-related conflict.

Contents

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1. Introduction

Conflict "is a difference within a person or between two or more people [or between groups of people] that touches them in a significant way" (LeBaron and Pillay, 2006: 12). Conflict often manifests itself in "expressed disagreements among people who see incompatible goals and potential interference in achieving these goals" (Peterson et al., 2013: 94). Yet, the expressed disagreements and perceived incompatibility may be become more entrenched due to a deeper-rooted social conflict that may have little to do with the expressed disagreement (Coleman, 2011; Jeong, 2008). When such conflict is present, the dialogue and decision-making processes need to account for it if the parties are to develop mutually supported solutions that can be sustained (Lederach, 2003). If not, any solution will be temporary, at best (Rothman, 1997).

Yet, even as the conservation field moves toward more collaborative governance models of engagement (Ansell and Gash, 2008; Leong et al., 2011; Reid et al., 2009), too often the processes used (or the individuals or organizations driving the process) fail to recognize or reconcile the deep-rooted conflict among stakeholders, and as a result, conservation goals are hindered (Balint et al., 2011; Clark and Slocombe, 2011; Dickman, 2010; Doucey, 2011; Peterson et al., 2013). This happens for two reasons: first, analysis is limited to the presenting disputes (and potentially common interests), and takes incomplete account of the deeper social conflicts often entangled in these disputes (Coleman, 2011; Deutsch and Coleman, 2012; Dickman, 2010; Jeong, 2008; Peterson et al., 2013). Without thorough analysis of these deeper social conflicts, stakeholder engagement processes often overlook (or exacerbate) this hidden dimension of conflict that, if accounted for, would help create the conditions for more sustainable long-term agreements (Jeong, 2008; Lederach, 1998; Levinger, 2013; Rothman, 1997). Second, there is a tendency to negotiate short-term, superficial solutions to these complex conflicts (Balint et al., 2011; Coleman, 2011; Dickman, 2010; Doucey, 2011; Fisher et al., 1991; Leong et al., 2009). In many cases, this tendency is due to a lack of capacity for employing more comprehensive approaches, a lack of mandate or willingness to change existing methods, or a desire to avoid the messy complexity of conflict that, on the surface, may seem tangential or irrelevant to the conservation mandate (Ansell and Gash, 2008; Coleman, 2011; DeCaro and Stokes, 2008; Leong et al., 2011; Manolis et al., 2009; Messmer, 2009).

Indeed, unmanaged or poorly managed conflict, including so-called human-wildlife conflict, represents an increasingly difficult obstacle to the effective management and conservation of many species of wildlife around the world (Madden, 2004; Michalski et al., 2006; Peterson et al., 2013; Redpath et al., 2013). In most cases, such conflicts stem from (or are exacerbated by) a deeper conflict between people and groups, not solely a conflict between people and wildlife—or even a conflict between people about wildlife. Yet, in many cases, the conflict with wildlife has become a symbolic manifestation of this deeper social conflict (Dickman, 2010). Conversely, despite the inherent complexity and depth of conflicts in most wildlife conservation and management contexts, they are often approached as transactional disputes that can be negotiated or resolved once common interests are established. Such limited approaches fail to acknowledge, engage, and respond to the deeper social and psychological dynamics between individuals and groups (hereinafter referred to as "social conflict") of which the immediate wildlife-related dispute represents only a surface manifestation (Burton, 1990; Dickman, 2010; Lederach, 2003; Rothman, 1997).

We argue that long-term conservation success requires deepening conservationists' capacity and strategies to include responses that seek to understand and address these more elusive social conflicts (Deutsch et al., 2006; Dickman, 2010; Peterson et al., 2013; Madden, 2004; Manolis et al., 2009). To do so, we propose a re-orientation of conservation's understanding of and approaches for addressing conflict through conservation conflict transformation (CCT). CCT principles and processes are adapted from the field of peacebuilding to the needs of conservation. CCT strives to positively transform often unseen and destructive social conflicts that underlie many conservation efforts but have, heretofore, largely remained blind spots undermining long-term conservation progress (HWCC, 2008).

This article begins by outlining the limitations of current conservation approaches and then highlights how CCT provides a more comprehensive means to analyze and address conflict. At its core, CCT is not just an approach and set of techniques, but a way of thinking about, understanding, and relating to conflict. This article provides an introduction to this alternate approach, including discussion of two models for analyzing conflict and framing interventions, and case studies that illustrate the impact of CCT in conservation initiatives.

2. Limitations of current conservation approaches

The field of conservation is rooted in biology. Conservation professionals typically enter the field because of an interest in understanding, protecting, or managing the needs of wildlife and wild nature—not humans. And, while the field is evolving, conservation efforts still tend to be focused on physical and spatial measures (e.g. use of fences or bee hives), economic fixes (e.g. incentives or payment of compensation for losses due to wildlife depredation or alternative livelihoods), technical solutions (e.g. changes in livestock husbandry or farming practices), legal actions (e.g. more stringent punishment and other stricter enforcement measures for laws prohibiting harm to wildlife), and biological methods (e.g. impacts on wildlife populations of lethal control) (Breck, 2004; Breitenmoser et al., 2005; King et al., 2011; Nyhus et al., 2005; Packer et al., 2013; Woodroffe et al., 2005). While these considerations are necessary for the success of conservation, we suggest they are insufficient when taken alone without addressing the psychological values and needs that drive social conflict (Balint et al., 2011, 2007; Dukes, 1999; Lederach, 2003; Leong et al., 2011, 2009; Peterson et al., 2013; Reed, 2008).

Conservation conflicts often serve as proxies for conflicts over more fundamental, non-material social and psychological unmet needs—including status and recognition, dignity and respect, empowerment, freedom, voice and control, meaning and personal fulfillment, identity (one's sense of self in relation to the outside world), belonging and connectedness, social, emotional, cultural, and spiritual security (Burton, 1990; Marker, 2003; Satterfield, 2002)—which are not addressed by the technical fixes or approaches described above. Indeed, conservation efforts often falter because they fail to fully account for the history, diversity and multiple levels of social conflict influencing conservation actions (Burton, 1990; Lederach, 2003; Madden, 2004; Marker, 2003).

Even when more effective stakeholder engagement is suggested or conducted, as in Barlow et al., 2010; Redpath et al., 2013; Treves et al., 2009, conservation practitioners may not have the skills or capacity to design and lead effective processes that transform destructive conflict into productive conflict (Leong et al., 2011, 2009; Manolis et al., 2009). Well-intentioned but poorly designed efforts may only address superficial aspects of the conflict and thus limit stakeholder receptivity to change and commitment to conservation goals (Leong et al., 2009; Reed, 2008). Without attention to the history of how previous decisions were made and implemented and the influence of deeper-rooted social and psychological factors in the conflict, the overall conflict may move further toward intractability, despite interventions that address the immediate or material issues at hand (Coleman, 2011; Deutsch and Coleman, 2012; Lederach, 2003, 1997; Naughton-Treves et al., 2003). The following case studies examining the conflicts with gray wolves in the United States (U.S.) and elephants in southern Africa illustrate how conventional conservation solutions fail to address the drivers of conflict and may result in the continuation and escalation of conflict (DeCaro and Stokes, 2008; Nie, 2004).

Eliminated from Montana, Idaho, and Wyoming by the 1930s, gray wolves began recovering in the 1980s (Bangs et al., 1998). Despite efforts to address livestock depredation by wolves through compensation programs, innovations in depredation deterrents, and many other conservation efforts, antagonism between pro-wolf and anti-wolf constituencies remained intense (Bangs et al., 2005; Chadwick, 2010; Nie, 2004, 2002).

Naughton-Treves et al. (2003: 1500) assessed the factors that influence tolerance of wolves and found that ‘deep-rooted social identity’ was among the most powerful predictors, while compensation for livestock losses had no influence on tolerance levels. Nevertheless, conservation and management have continued to focus on compensating losses, educating livestock owners in preventive measures, providing technical support to implement such measures, and using lethal control (Bangs et al., 2005; Breck, 2004; Musiani et al., 2004). If the physical threat to and economic value of the livestock were the only concerns, affected livestock ranchers' concerns would be sufficiently addressed by these material and economic solutions. Unfortunately, technical assistance and compensation have remained ineffective (Naughton-Treves et al., 2003; Nyhus et al., 2005); as one Idaho rancher commented, “compensation does not equal reconciliation” (Ellis et al., 2005). This rancher's comment hints at the social, psychological, cultural, political, and legal history and sentiment shaping his attitudes and understanding of the conflict (Nie, 2003). Ed Bangs, the wildlife biologist who led the U.S. federal government's northern Rockies wolf recovery effort from 1988 until 2011, stated that wolf management is “all about humans and their values, and how we use symbols to discuss our values with other people” (Ring, 2011: 2). Bangs further asserted: “We've done way too much wolf-handling and radio-collaring. In [addressing the conflict], there's a predictable pattern people go through: They become distracted from real issues and problems... and the use of technology is seen as the fix for everything” (Ring, 2011: 2).

Another set of examples illustrate how conservation outcomes can depend on whether or not the social-psychological needs and conflicts of a community are addressed as part of the development and implementation of conservation solutions. In successful efforts to secure community commitment to implement and maintain various fencing solutions to prevent human-elephant conflict, conservationists report spending more time asking questions of and listening to the community members, building trusting relationships, supporting creative and positive identity-building events within the community, and not only regularly engaging with communities, but empowering them in a leadership role during the decision-making and implementation process (Osborn and Parker, 2003; Zimmermann et al., 2009). Thus, before a solution was arrived at, it is likely that enough of the social-psychological drivers of conflict were understood and addressed, so that when solutions were decided upon, there was greater motivation and commitment by the community to maintain these solutions (DeCaro and Stokes, 2008; Engelberg and Kirby, 2001). Not surprisingly, as these ‘ready-made’ technical solutions were rapidly deployed to other communities experiencing human-elephant conflict (often with short funding cycles pushing for early implementation and testing of tactical solutions), there was less time and attention given to the relationship and process components that would help transform the social conflict. As a result, in many cases, because the communities' social-psychological needs were ignored, these communities resented the imposed solution, and failed to implement or maintain the chili peppers or tore down wire from fences to use for other purposes, including illegal snaring (Bird, pers. comm., 2013; Sitati and Walpole, 2006; Songhurst, 2010).

In such cases, we argue, conservation setbacks often stem from a lack of consideration of the full spectrum of the conflict and an over-emphasis on the immediate material and economic factors impacting conservation. This emphasis relies, implicitly, on Abraham Maslow's “hierarchy of needs” (Maslow, 1954). Maslow's theory posits that until one's basic physiological (food, water, shelter, sleep) and security (physical, employment, health, property) needs are met, humans are less concerned with or do not seek out the ‘higher level’ social and psychological needs. However, despite its popularity, Maslow's framework has been repeatedly refuted by scholars from a variety of disciplines and fields, including sociology, psychology, peacebuilding, and economics (Burton, 1990; Clark, 1990; Coate and Rosati, 1988; Galtung, 1990; Max-Neef et al., 1989).

Beyond the narrow focus on addressing the material losses, analyzing the conflict dynamics and developing appropriate decision-making processes that address these deeper drivers of conflict would build genuine community receptivity to, commitment in, and ownership of the solutions (Frahm and Brown, 2007; Lachapelle, 2008; Senge, 1997). Better understanding and accounting for the social conflicts as part of conservation efforts would likely prevent or overcome obstacles and help create conditions for greater receptivity and ownership by the very group who must be responsible for maintaining solutions (Jackson et al., 2001; Smith and Torppa, 2010). From a conservationist's point of view, the seemingly self-destructive behavior of communities that do not take action to help themselves alleviate wildlife damage to their property is frustrating and disheartening. Yet, a closer examination of the social conflicts underpinning conservation offers explanations for seemingly enigmatic behavior, providing the practitioner with a starting point to either prevent such incidents, or if they have already occurred, to use them as opportunities to intervene more effectively in the future (Lachapelle, 2008; Lederach et al., 2007; Lederach, 2003).

3. Conservation conflict transformation

3.1. What is conflict transformation?

Conflict transformation (CT) is

> “a capacity to envision ...[and] a willingness to respond [to]...conflict positively, as a natural phenomenon that creates potential for constructive growth. Change is understood both at the level of immediate presenting issues and that of broader patterns and issues... Conflict transformation focuses on the dynamic aspects of social conflict. At the hub of the transformational approach is a convergence of the relational context, a view of conflict-as-opportunity, and the encouragement of creative change processes.”
>
> [Lederach, 2003: 15.]

Conflict is an inevitable outcome of human interaction (Burton, 1987). It is the consequences of conflict that determine whether it is constructive or injurious (Lederach, 1997). CT offers a distinct theory and approach to conflict that evolved out of a re-conceptualization of traditional theories and approaches in order to be more applicable to today's conflicts (Miall, 2004). Contemporary conflicts are often deep-rooted, protracted, interconnected at micro and macro scales of conflict, and characterized by power and status asymmetries (Miall, 2004). Conflict transformation approaches conceptualize immediate problems as opportunities to understand and positively change the causal relationships, decision-making processes, and systems shaping the conflicts (Lederach et al., 2007). In this way, conflict transformation addresses both the presenting problem and the deeper social conflicts with the goal of establishing sustainable conflict transformation mechanisms to address future conflicts.

Many conservation conflicts involve deep-rooted conflict. Such conflicts include deeply held values, high stakes, power imbalances, complexity, and a sense of moral superiority that may drive parties to perpetuate the fight, even when they cannot win in the short term (Burgess, 2004; Clark, 2002; Pearce and Littlejohn, 1997). Non-negotiable social and psychological needs are often at the root of conflicts that may appear on the surface to be negotiable (Burton, 1993, 1990). When threatened, identity needs, in particular, produce significant negative reactions (Lederach, 1998; Rothman, 1997). Deep-rooted conflicts often have conflict both within groups (intragroup) and between groups (intergroup), where the internal conflict actually perpetuates the external conflict, as leaders are compelled to maintain the conflict in order to protect their identity and promote group cohesiveness (Deutsch and Coleman, 2012; Deutsch, 1973).

Like other deep-rooted conflicts, many conservation conflicts often have a contentious history that adds meaning and emotion to each new dispute, deepening both sides' positions against, and negative views of, each other. Within this history, there is also often long-standing inequity where low-power groups have traditionally been disadvantaged by the basic social structure of society (Coleman, 2006). Deep-rooted conflicts are perceived by disputants to be seemingly intractable and hopeless, presenting no way out. This perception is significant because it informs action. Negative perceptions lead to negative actions, thus perpetuating conflict (Deutsch and Coleman, 2012; Deutsch et al., 2006). Paradoxically, deep-rooted conflicts often cause disputants to harm themselves and the things they value in an effort to ensure their opponent does not win (Atran and Axelrod, 2008).

Unlike many traditional conflict management approaches, CT approaches strive to move beyond the obvious dispute, focusing on the social, psychological, and systemic root causes of conflict. Further, CT advocates long-term and sustained engagement with the parties in conflict—a contrast to many conflict resolution and stakeholder engagement approaches, which typically engage in episodic periods of engagement around solving a specific and limited problem (Lederach, 2003).

Another unique aspect of CT is that it starts with a focus on the relationships and the relational context (Lederach, 2003). By designing and sustaining processes that aim to reconcile negative relationships, CT approaches seek to create conditions where actors can humanize their view of and relationships with "the other" to create the space and opportunity to move from an "us" versus "them" mentality to a more inclusive and genuine "we". By empowering diverse participation, including actors and groups usually marginalized or minimalized in such deliberations, unilateral agenda-setting or decision-making are replaced by a collaborative environment that addresses many of the power inequalities that underpin broader social conflicts and provides the space and opportunity for risk-taking and creativity (GCCT, 2014; Lederach, 2010; Lederach, 2003; Ramsbotham et al., 2011).

Conflict is a fundamental part of society's continual progression, not an isolated incident (GCCT, 2014; Lederach, 2003). Complex, deep-rooted conflicts are often defined and reinforced by the connectivity between micro-conflicts, at the individual or local scale, to macro-conflicts, at the systemic, regional, or global level (Hendrick, 2009). As such, CT embraces the unique complexity of each conflict context and so relies on an adaptable and replicable set of theories, principles, processes, and skills, rather than a highly prescriptive, step-by-step formula for stakeholder engagement. We argue that these conditions for engagement are essential if conservationists are to adapt and evolve with the inevitable changes in the socio-political and ecological systems in which they work. We further suggest that conflict transformation's long-term, systemic approach is better suited to conservation as both are engaged in multi-level, long-term strategic change.

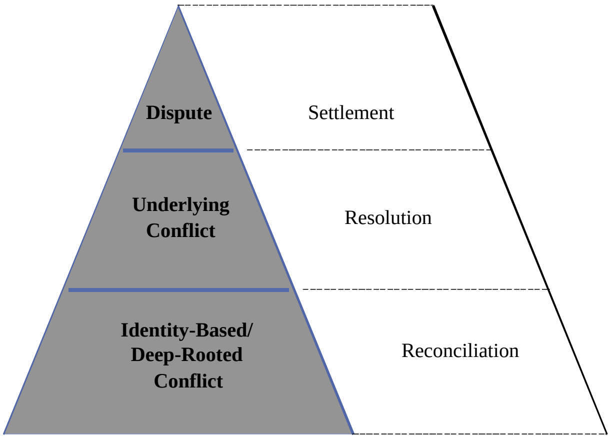

Fig. 1. The three levels of conflict that may exist in the conflict context (and the corresponding process used to address conflict at that level). Source: Adapted from Canadian Institute for Conflict Resolution (2000, 73).

3.2. Conservation conflict transformation

Conservation conflict transformation (CCT) applies CT to conservation contexts. Two models provide useful frameworks to identify and orient the practitioner to how they might address the drivers of social conflicts that CCT seeks to transform. The Levels of Conflict model (CICR, 2000) is an analytical tool we use to explore the severity and types of conflict present in a conservation conflict context. This model helps the practitioner analyze and describe the root causes of a conflict so that the subsequent intervention can address both the visible and deeper, less visible sources of conflict. The Conflict Intervention Triangle is a practical adaptation of earlier models by Moore (1986) and Walker and Daniels (1997). This model provides an orientation for planning to ensure consideration of the full range of potential sources of conflict and points of intervention.

3.2.1. Levels of conflict: An analytical model

The Levels of Conflict model enables analysis of the complexity, scope, and depth of conflict in a given setting. This model classifies three levels of conflict: disputes, underlying, and identity-based (CICR, 2000).

The first level of conflict—the dispute—is the obvious, tangible manifestation of a conflict (see Fig. 1). It is the immediate (usually material) issue seemingly at the 'center' of the conflict. For instance, a dispute could center on a disagreement over cattle grazing rights on public land; a conservation proposal for invasive species eradication that is rejected by the community; or a disagreement over preferred solutions to address livestock depredation by endangered predators.

To illustrate conflict at the dispute level, imagine a car accident between two strangers who find themselves in a minor fender-bender.[1] Addressing this dispute is relatively straightforward:

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[1] This analogy was first developed by Dr. Vern Redekop in a seminar entitled, 'Deep-Rooted Conflict Theory.'

repairing the damaged vehicles and determining who is going to pay. (We will return to this analogy below).

Conflicts can exist solely at the dispute level, but more typically a dispute is also the surface expression of deeper levels of conflict. A narrow focus on the 'dispute' level explains, in part, why conservation practitioners are sometimes surprised that conflict remains or even escalates after the problem appears to have been 'settled.'

The second level of conflict that may exist in a specific conflict context is underlying conflict. Underlying conflict is a history of unresolved disputes. Its existence in a conflict context would imbue any current or recent dispute with added significance that is not necessarily obvious from the bare 'facts' of the current incident alone. Underlying conflict results from past interactions between, or decisions made by, the same parties that intensify or aggravate the present situation. The importance of this history may be further obscured because the participants themselves may find it easier to focus on and articulate a specific, concrete, economic, or physical loss, than to express more complex social or psychological issues (e.g. resentment about how past decisions by authorities were made that may exacerbate the meaning of a new incident).

To illustrate underlying conflict, imagine a similar car collision. But, in this case, the drivers are not strangers; they are a couple who recently finalized an acrimonious divorce. When they get out of the car and recognize each other, we probably understand that the conflict dynamic is very different from what played out between the two strangers. Since there is underlying conflict between this couple, the car accident is likely no longer just about a bent fender. The car repairs (and who is to blame for it) may become an opportunity to 'right' past perceived injustices. While the drivers in the first example might typically exchange information about damage and insurance, we can expect a wider range of possible reactions from our divorced couple, with a greater potential for escalation or repercussions.

In disputes with underlying conflicts, each new incident carries with it meanings derived from past interactions. These meanings are not necessarily the same for all parties. As long as one person in the dispute feels that previous disputes remained unsatisfactorily resolved, underlying conflicts distort the dynamics around the incident. In conservation, it is nearly impossible to avoid some element of underlying conflict since conservation efforts typically involve years, if not decades, of decisions and actions to study or conserve wildlife within or near human communities.

The third level of the model—identity conflict—involves values, beliefs, or social-psychological needs that are central to the identity of at least one of the parties involved in the conflict. Burton (1984: 212) explains it this way: "when the non-material identity needs of a people are threatened, they will fight." In these cases, the disputant(s) feel that the stakes are so high that they are willing to take extraordinary measures to 'win.'

Let us return to our car collision analogy to explore the implications of identity-based conflict. In this scenario, the car accident takes place in Bosnia and Herzegovina during the aftermath of the war in 1996. By the conclusion of the fighting, authorities of the three communities ensnared in the civil war—Serbs, Croats, and Bosniaks—issued their own car license plates to distinguish between the different groups. Imagine our car accident again, except this time when the drivers scramble out of their vehicles, each finds that the other car has the 'wrong' license plate on it. The tension will, most likely, far exceed either of the previous examples. Our drivers may never have met each other or have personal history. Yet, they are likely to make prejudicial assumptions and judgments based on the other's group affiliation and may ascribe responsibility to the other individual for past actions taken by other members of their group (sometimes generations before). This additional layer of conflict contributes greater intensity and complexity to the presenting situation.

Intense animosity between individuals based on group or social identity is not unique to civil war. Many conflicts in conservation also involve deeply rooted values, needs, and beliefs, in which one group's identity may actually be defined in opposition to another's because of perceived threats to their identity or way of life. For example, a conservation organization's presence and resources devoted to wildlife needs may be perceived as ignoring or slighting the physical and social needs of the local community (Madden, 2004). Ranchers or hunters may experience national wildlife protection laws as an infringement upon their sense of autonomy (Clark et al., 2010; Simon, 2013). For conservation professionals whose identity is focused on the conservation of wildlife, actions that threaten to extirpate a species may be considered a profound moral violation.

The above examples illustrate intergroup identity conflict, but intragroup conflict also offers examples of identity conflict. Conservation organizations and professionals may perceive others within their field, or even within their organization, as a threat to their ability to realize their potential or attain recognition for their work. Hunters, while often lumped together as single group, often contain conflicting sub-groups, including members who divide themselves along pro- or anti-predator conservation lines or define themselves as anti-government and pro-government advocates. As diverse as human nature is, so are the possible manifestations of identity conflict.

Analyzing wildlife conservation conflicts with the Levels of Conflict model might reveal, for example, that a dispute about livestock depredation, crop damage, or the legal determinants for wildlife management is fueled by underlying and identity issues. Or it may suggest that a conflict that began as a material dispute has evolved into an identity conflict over time, as those involved invest themselves more in the dispute and come to identify themselves and their group with their positions in the dispute (Lederach, 1997). Eventually, these identity conflicts become so deep-rooted that they become an integral part of a person's or group's identity. This identity-based level of conflict is intense and complex, and may appear 'irrational' compared to the specific current conditions or material issues in question.

The energy, effort and processes needed to address these different levels of conflict differ greatly. Dispute level conflicts, if that is all that exists, can be solved relatively simply once the isolated incident is rectified. The model employs the term 'settlement' to describe efforts to solve the problem at the dispute level. Disputes in society are often settled in courts using a rights-based system with legal codes for determining responsibilities, evidence, and outcomes. Conservation groups use lawsuits tactically, for example, to stimulate or halt government management actions. (Yet these lawsuits are often both a symptom and cause of deepening conflict.) Similarly, governments use existing laws as a means to ensure compliance. Compliance with a 'settlement' by a stakeholder may settle the immediate dispute; but, if deeper levels of social conflict exist and are not addressed, settlements are only temporary and those involved will likely use (or create) another opportunity to redress perceived injustices.

The levels of conflict model uses the term 'resolution' to describe efforts to solve underlying conflicts, while 'reconciliation' is used to reflect the shift in identities of the disputants necessary to address identity-based conflicts. The temptation is often to ignore or disregard these social conflicts in stakeholder decision-making processes as they do not appear to be directly related to, or are believed to be outside the purview of, conservation (Dickman, 2010).

Even new actors, stakeholder groups, approaches and tools are likely to be affected by the deep-rooted conflicts associated with previous or related people, groups or efforts, with the result that new disputes may be articulated in the familiar vocabulary of preexisting conflicts, and new actors may be subject to the same reactions and prejudices of their predecessor. Research suggests that when deeply-held core values are involved, the intensity of opposition can actually increase rather than diminish when the deeper-rooted conflicts are ignored and material incentives (dispute level tactics) are offered as a compromise (Ginges et al., 2007).

While disputes tend to be tangible, material, and easily identifiable, underlying and identity-based levels of conflict are often ambiguous, intangible, and either unspoken or responded to ineffectively. Underlying and identity-based conflicts may find expression as a dispute because expressing these deeper-rooted conflicts as a dispute gives tangible focus and clarity to a group's concern (Rothman, 1997). It may also be easier or more socially acceptable to speak of, or respond to, material losses or a specific incident, rather than deeper emotional or psychological needs or injuries (Sites, 1990). Finally, the inherent focus of conservationists tends to steer dialogue toward the wildlife itself (or ecosystems) and away from the impact that conservation decisions and actions may have on a person's psychology, culture, beliefs, values, or history (Clark, 2002; Dickman, 2010; Madden, 2004; Redpath et al., 2013).

3.2.2. The conflict intervention triangle: Planning interventions

The Conflict Intervention Triangle model provides a conceptual orientation to conflict intervention planning. Our adaptation of the Conflict Intervention Triangle provides a useful framework for relating three dimensions of conflict: process, relationships, and substance (Moore, 1986; Walker and Daniels, 1997). Moore's original version of this triangle and Walkers and Daniels' adaptation both use the term "procedural" instead of "process." By definition, 'procedure' suggests there is an official or established way of doing something. 'Process,' on the other hand, implies a series of actions to achieve a goal, and we believe this term more accurately captures the flexibility and adaptability needed to navigate the complexity of conflict. Moore originally used the term "psychological" instead of "relationships," yet given the numerous psychological needs that can be addressed through a good process and recognizing the significance of individual and group relationships in shaping a conflict outcome, we prefer to use "relationships," consistent with the Walker and Daniels model.

By visualizing the three aspects of conflict intervention in this model, one can more easily resist the impulse to focus only on dispute level solutions, recognizing that the processes and relationships of any intervention require equal attention (see Fig. 2). In fact, while all three aspects of conflict are important, the process and relationship dimensions of a conflict intervention offer a greater opportunity to address underlying and identity-based conflicts.

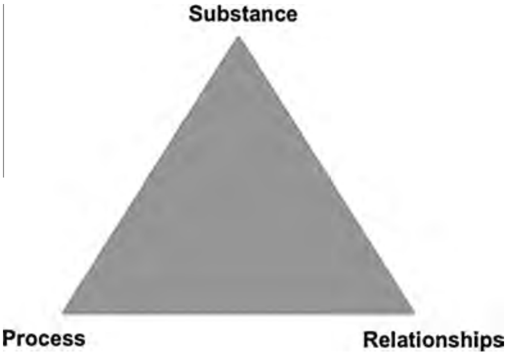

Fig. 2. Conflict intervention triangle model showing the three potential sources for conflict and three dimensions of conflict intervention essential for the transformation of conflict. Adapted from Moore (1986) and Walker and Daniels (1997: 22).

Of the three sets of factors aligned with the points of the triangle in Fig. 2, 'substance' is the most straightforward and largely corresponds to the dispute level conflict in the Levels of Conflict model.

Process factors relate to decision-making design, equity and authority, and how (and by whom) these are exercised. For instance, parties might agree with the merits of a particular solution, but if they do not feel their concerns or input were sufficiently recognized in the process, they may reject any decision reached, even a decision to employ a solution that addresses their substantive concerns. Conversely, parties are more likely to accept decisions not fully in line with their views or values if they felt genuinely respected and invested in a decision-making process (Fisher et al., 1991; Reed, 2008; Leong et al., 2009).

Recent research findings from the business sector support the claim that the quality of the decision-making process influences the durability and success of solutions (Lovallo and Sibony, 2010). Researchers reviewed 1,048 critical business decisions over five years, and found that "process mattered more than analysis [of potential solutions] in determining the quality of outcomes, by a factor of six" (Lovallo and Sibony, 2010: 6).

Effective decision-making processes not only increase the innovation and durability of solutions, but they also strengthen relationships between participants. Improved communication and trust in relationships increases the likelihood that future problems will be addressed more effectively, and that previous solutions can be more easily adapted to changed circumstances (Ansell and Gash, 2007; Reed, 2008).

In designing processes, conservationists and governments often resist giving up decision-making control, because they already have the law on their side or they may fear what will happen when stakeholders who seem less committed, or even antagonistic to conservation objectives, are given a legitimate voice in decision-making. They understandably fear that involving other stakeholders in decision-making around wildlife risks unacceptable compromise or loss of control in conserving species and spaces (Leong et al., 2009; Rudolph et al., 2012). Yet, anecdotal reports from conservationists and government leaders that use CCT approaches suggest that instead of having to live with less than desirable trade-offs, they can actually expand the range of win–win solutions by addressing these deeper-rooted social conflicts (Beggs, 2012; Booker and Maycock, in press; Cullens pers. comm., 2013; Gotliffe pers. comm., 2013; Kenyon pers. comm., 2013; Lewandowski, 2015; Mupunga pers. comm., 2012; Odorkot pers. comm., 2012; Tembo pers. comm., 2013). More rigorously assessed, longer-term application of conflict transformation principles in other fields support these anecdotal findings (Anderson and Olson, 2003; Hendrick, 2009; Lederach et al., 2007; Lederach, 2003, 1997; Smock and Serwer, 2012).

The third side of the conflict intervention triangle is 'relationships.' The relationship factor of conflict interventions is most easily illustrated in personal conflicts between individuals where the quality of a relationship or the level of respect and trust that exists between two people can itself become a source of contention. A lack of trust can be extended to include group relations as well. Identity-based conflicts find their expression in the relationship among communities, between a community and conservation authorities or the state, or even between conservation groups competing with one another toward the same conservation goals. In our experience, the relationship basis for conflict is too often ignored, avoided, or treated too lightly by conservation and government authorities who label other groups as 'partners in conservation' when that relationship is still wrought with distrust. Experience suggests that stakeholders will undervalue or even sabotage conservation solutions offered to solve immediate conservation issues if they do not also meet deeper social and psychological needs, including those met through relationships (Satterfield, 2002). Yet, by the same token, the time and effort spent developing individual relationships, particularly across the lines of conflict, can help catalyze broader, positive social change (Lederach, 2005; Wheatley, 1998).

Conserving wildlife today requires a change in orientation to and understanding of conflict, as well as the capacities and approaches needed to achieve long-lasting success. A good process gives attention to the dialogue and relationship-building needed to foster dignity, respect, and trust among stakeholders, as well as to support more effective decision-making around and commitment to tangible solutions. A good process will create the space and opportunity for a reconciliation of deep-rooted social conflicts that make reaching and sticking to a decision about a dispute more viable. Too often in the urgency to save imperiled species, we rush to create solutions through processes that fail to transform the roots of social conflict and thus fail to shape the relationships necessary for long-term success. By contrast, the CCT approach advocates ‘going slow to go fast’ (Ury, 1991). To that end, giving attention to the decision-making process and relationship components of a conservation conflict is as important as attending to the substance of the conservation solution and improves the chances of long-term success. (Hicks, 2001; Lederach et al., 2007; Lederach, 2005; Walker and Daniels, 1997).

3.3. Conservation conflict transformation in action: Two case studies

The following two cases demonstrate both the versatility and replicability of conflict transformation in different contexts. The first case involves a multi-stakeholder intervention that included capacity building in conflict transformation. The second case illustrates conflict transformation led by a conservation leadership team after participating in a capacity building workshop. Although CT relies on a replicable set of principles, skills, theories, and processes rather than a formulaic process, we believe that one of the best practices in transforming conflict involves building the capacity of conservation teams and diverse stakeholders (Lederach, 1997; Manolis et al., 2009). First, capacity building in conflict transformation imbeds and sustains a suite of capacities within the people, institutions, and groups engaged in a conflict and responsible for its continual transformation. Second, capacity building builds awareness among stakeholders of their role in creating or perpetuating conflict, as well as their power to transform it. And finally, capacity building provides a safe and neutral setting in which to create ‘small wins,’ build trust, and foster a greater motivation to work constructively together (Ansell and Gash, 2007; Brown, 2003). The following cases offer only a partial exploration and explanation of the complexity, challenges, and positive changes that resulted.

The first case involved a state-level stakeholder conflict in a western U.S. state over mountain lion management and public safety. The conflict was largely between a state government agency and several wildlife conservation non-governmental organizations (NGOs). At the dispute level, the groups disagreed over how public safety incidents were being handled and whether a “shall kill” designation (which mandated lethal control as the only option) was appropriate in all cases of public safety. Beyond this dispute the NGOs felt marginalized from decisions around mountain lion management and the government agency felt unfairly and negatively targeted by some NGOs’ use of legal action and the media. In sum, the stakeholders did not trust one another, and became suspicious of and isolated from each other. Poor communication and very limited information sharing characterized their relationship. Any action or communication by one group toward the other, even well-intentioned, was easily misconstrued and mistrusted. Although the necessary science of mountain lion behavior and biology was available, there was little social capacity to use and apply that information to collaboratively improve current wildlife responses to public safety incidents. As a result, when a new public safety incident with mountain lions occurred, the management response improved little and stakeholder relationships continued to degrade. And, while the stakeholders focused their reactions on the new incident, the history of unresolved disputes influenced their reactions. The identity-based conflict manifested itself as an “us versus them” stance with parties making prejudicial assumptions about members of the other group simply based on their institutional affiliations.

Following a particularly controversial public safety incident at the end of 2012, a state legislator proposed new legislation to add flexibility in the use of non-lethal control in response to public safety incidents. Further, the proposed legislation mandated that the government agency would now share responsibility with other wildlife experts within the state when responding to these difficult situations. To be clear, the government staff involved in the 2012 incident wanted assistance and additional flexibility in handling the situation, but believed their hands were tied by existing rules that prevented them from seeking assistance or using any means other than lethal control. That said, once the new legislation was proposed, staff from the government agency felt “punched in the gut” (Kenyon, pers comm, 2013). Although the legislation would give them greater flexibility and access to resources, agency personnel opposed the proposed law due to the “us versus them” depth of social conflict that existed (Riske, pers comm, 2013).

Within three months of the precipitating crisis, in early 2013, government and NGO stakeholders in the conflict participated in a five day capacity building conflict intervention and planning process facilitated by HWCC. What resulted was a humanizing of “the other” and reconciliation of relationships that were previously undermined by underlying and identity conflict. This enabled the development of productive, trust-based relationships among the stakeholders. In turn, those relationships helped foster the creation of a new problem-solving method designed to generate and implement wildlife response solutions; formally sustain and nurture stakeholder relationships; and institutionalize a creative, equitable, and transparent decision-making process. Within four months of the workshop, a senior scientist for the government agency reported that “lion management is now moving forward after decades of stalemates because of our implementation of CCT principles and practices. We’re now getting to a point where we’ve wanted to be for over 40 years…and on an easier road.” The other stakeholders agreed (Madden et al., 2013). A six month evaluation of their progress found that a significant indicator of success was that when successive challenges arose, the trust and capacity of these individuals and groups to work together grew and deepened. Indeed, in a short period of time, this group transformed a decades-long cycle of entrenched conflict into effective shared problem-solving and mutual trust and respect.

The second case took place in an area of Africa that has experienced dramatic increases in elephant poaching and trafficking partly due to porous and corrupt borders, extreme poverty and isolation, and increased access following establishment of a foreign timber concession in the area. A team from a small conservation organization manages a 600 square kilometer concession within the larger reserve. Despite the organization’s good relationships with the communities and dedication to developing alternative livelihoods, providing education, and improving law enforcement, poaching continued to increase. The leadership team participated in a conflict transformation capacity building workshop in 2012 and immediately put their skills and capacities to the test.

At the time of the conflict transformation capacity building workshop, the conservation organization was training community members to become anti-poaching scouts in the concession. A few weeks after the CCT workshop, the scouts were ready to graduate and the conservation organization held a graduation ceremony and party, and invited all the villagers and their chiefs. One chief spoke eloquently about the need for conservation and the importance of putting an end to poaching and snaring. The next day the scouts went out on their first anti-poaching patrol and they found snares. The evidence led them back to the same chief who made the eloquent pro-conservation speech the day before. When they went to the chief, who is a powerful shaman for a community that believes strongly in the spirit world, he threatened to put a curse on them that would result in death to them and their families if the scouts arrested him. Word spread quickly, and other villages and chiefs were angry and emotional about this incident. Suddenly, the entire project reached a crisis. If the scouts arrested the chief, they and their families might be killed. If they didn't, it would undermine the credibility of the project and the organization. The conservation team recognized that the anti-poaching project could only succeed if the entire community was fully behind all decisions. So, instead of providing solutions, the conservation team developed a process to bring the communities together and empowered them to make the decision. Having the community develop the solution gave them ownership over it. Eventually, another village chief suggested an amnesty in which all the villagers and chiefs would turn in their snares over the next two weeks and after that time anyone caught snaring or poaching would be arrested, chiefs and villagers alike. Everyone agreed. Over the next two weeks, for the first time in the history of the reserve, villagers and chiefs—including the previously-caught chief—turned in their snares voluntarily (Beggs, 2012).

In the following months, the conservation team applied CCT principles in other projects, including using an education center to train the community in skills they wanted to learn. The community asked to learn construction skills because they wanted to build a mosque. A narrow, linear view of conservation might suggest that building a mosque is a waste of conservation resources. Yet, building the mosque brought the community together and it met and strengthened their non-material needs for spiritual security, meaningful engagement, and connectedness. In supporting these social, spiritual, and psychological needs of the community, the conservation team gave dignity and respect to the deepest values and beliefs of the community. In turn, the conservation team earned the community's respect, trust, and allegiance. The social cohesion that resulted translated into a desire and strength to resist negative outside influences that would corrupt the integrity of their community, such as pressure to poach elephants.

As a result, during a period of time where elephant poaching and trafficking skyrocketed in the surrounding reserve (with 2–3 elephants killed per day), this 600 square kilometer concession lost only 8 elephants total in the same year, due to poachers from outside the community. This represented a significant reduction in poaching from the year before and a significant contrast to the area outside this project's jurisdiction. In addition, the villagers started actively pursuing suspected poachers and ensuring their arrest, while simultaneously treating the suspect in a dignified and respectful way. In the rest of the reserve, poachers are still rarely, if ever, turned into the police (Beggs, pers comm, 2013).

4. Conclusion

Conservation conflict transformation (CCT) enables the development of innovative, durable solutions through analyses and processes that simultaneously help reconcile negative relationships and transform the political, social, or economic structures and systems—the enabling environment—impacting conservation efforts. CCT recognizes the natural ebb and flow of conflict, and as such, is a dynamic, continually evolving opportunity for creativity through and evolution of relationships (Lederach, 2005, 2003). The continual engagement that maintains constructive and positive relationships and decision-making processes allows conservation efforts to adapt more effectively to ongoing changes in social and ecological systems.

Successful integration of conflict transformation into conservation requires analysis of all levels and sources of conflict within the social system in which conservation is embedded. Such a thorough analysis is an essential first step to avoid unintended consequences and foster social conditions that support decision-making directed toward sustainable conservation (Hendrick, 2009; Lederach, 1997; Lederach et al., 2007).

We argue that conservation efforts would benefit from improved capacity and resources for understanding and transforming the complex drivers of deep-rooted social conflicts impacting wildlife conservation and management actions. HWCC is currently leading efforts to integrate CCT in wildlife conservation efforts, and is being joined by a growing list of organizations whose staff and leadership have developed their capacity for and moved to embed CCT principles in the operation of their organization and projects. Moreover, as recognition of the interactions between conservation and social conflict (including warfare and organized crime) grows, more governments, peacebuilding institutions, universities, wildlife conservation organizations, sustainable development institutions, and others are moving to better understand and respond to the challenges, opportunities, and systemic connections present in these complex conflicts (Dudley et al., 2002; Gibbs et al., 2010; Hanson et al., 2009; Wellsmith, 2011). As our community of practice grows, we look forward to learning from and supporting one another in advancing the field.

To that end, a more systematic assessment of CCT's merits and impacts is needed. Nevertheless, the last few years of anecdotal evidence suggest that integrating CCT into conservation efforts can make a significant, positive difference. As our society's social carrying capacity for wildlife depends on conservation's ability to reconcile social conflicts impacting wildlife conservation, we hope that these tools and approaches can continue to contribute to innovative solutions to long-standing conservation challenges.

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References

Anderson, M.B., Olson, L., with assistance from Kristin Doughty, 2003. Confronting War: Critical Lessons for Peace Practitioners. The Collaborative for Development Action, Inc.

Ansell, Chris, Gash, Alison, 2008. Collaborative governance in theory and practice. J. Public Admin. Res. Theory 18 (4), 543–571.

Atran, Scott, Axelrod, Robert, 2008. Reframing sacred values. Negotiation J. 24 (3), 221–246.

Balint, P., Stewart, R., Desai, A., Walters, L., 2011. Wicked Environmental Problems: Managing Uncertainty and Conflict. Island Press, Washington, DC.

Bangs, E.E., Fritts, S.H., Fontaine, J.A., Smith, D.W., Murphy, K.M., Mack, C.M., Niemeyer, C.C., 1998. Status of gray wolf restoration in Montana, Idaho and Wyoming. Wildlife Soc. Bull. 26 (4), 785.

Bangs, Edward E., Fontaine, Joseph A., Jimenez, Michael D., Meier, Thomas J., Bradley, Elizabeth H., Niemeyer, Carter C., Smith, Douglas W., Mack, Curt M., Asher, Val, Oakleaf, John K., 2005. Managing wolf-human conflict in the northwestern United States. In: Woodroffe, Rosie, Thirgood, Simon, Rabinowitz, Alan (Eds.), People and Wildlife, Conflict or Coexistence? Cambridge University Press, Cambridge.

Barlow, Adam C.D., Greenwood, Christina J., Ahmad, Ishtiaq U., Smith, James L.D., 2010. Use of an action-selection framework for human-carnivore conflict in the Bangladesh Sundarbans. Conserv. Biol. 24 (5), 1338–1347.

Beggs, 2012. Wildlife conflict management. In: Practive in Mozambique. Wildlife Conservation Network Newsletter, Fall, 2012.

Blackstock, K., Kelly, G., Horsey, B., 2007. Developing and applying a framework to evaluate participatory research for sustainability. Ecol. Econ. 60, 726–742.

Breck, Stewart W., 2004. The importance and process of research in the search for coexistence. In: Fascione, Nina, Delach, Aimee, Smith, Martin (Eds.), People and Predators: From Conflict to Coexistence. Island Press, Washington, DC.

Breitenmoser, Urs, Angst, Christof, Landry, Jean-Marc, Breitenmoser-Wursten, Christine, Linnell, John D.C., Weber, Jean-Marc, 2005. Non-lethal techniques for reducing depredation. In: Woodroffe, Rosie, Thirgood, Simon, Rabinowitz, Alan (Eds.), People and Wildlife, Conflict or Coexistence? Cambridge University Press, Cambridge.

Brown, Mark Malloch, 2003. Democratic governance: toward a framework for sustainable peace. Glob. Gov. 9, 141–146.

Burgess, Heidi, 2004. High-stakes distributional issues. In: Burgess, Guy, Burgess, Heidi (Eds.), Beyond Intractability. Conflict Information Consortium. University of Colorado, Boulder.

Burton, John W., 1984. Global Conflict. Wheatsheaf, Brighton.

Burton, John W., 1987. Resolving Deep-rooted Conflict: A Handbook. University Press of America, Lanham.

Burton, J., 1990. Conflict: Basic Human Needs. St. Martin's Press, New York.

Burton, John, 1993. Conflict: Human Needs Theory. St. Martin's Press, New York.

Canadian Institute for Conflict Resolution, 2000. Becoming a Third-Party Neutral: Resource Guide. Ridgewood Foundation for Community-Based Conflict Resolution (Int'l).

Chadwick, Douglas, 2010. Wolf Wars. National Geogr. 217 (3), 34–55.

Clark, M., 1990. Meaningful social bonding as a universal human need. In: Burton, J.W. (Ed.), Conflict. St. Martins Press, New York.

Clark, Tim W., 2002. The Policy Process: A Practical Guide for Natural Resource Professionals. Yale University Press, New Haven, CT.

Clark, Douglas A., Slocombe, D. Scott, 2011. Grizzly bear conservation in the foothills model forest: appraisal of a collaborative ecosystem management effort. Policy Sci. 44 (1), 1–11.

Clark, Susan G., Hohl, Aaron, Picard, Catherine, 2010. Pursuing large scale conservation in the common interest: a perspective. In: Clark, Susan G., Hohl, Aaron, Picard, Catherine, Newsome, Darcy (Eds.), Large Scale Conservation: Integrating Science, Management, and Policy in the Common Interest. Yale School of Forestry and the Environment, New Haven, CT.

Coate, Roger A., Rosati, Jerel A., 1988. The Power of Human Needs in World Society. Lynne Rienner Publishers, Boulder, CO.

Coleman, Peter, 2006. Intractable Conflict. In: Deutsch, Morton, Coleman, Peter (Eds.), Handbook of Conflict Resolution. 2000. Jossey-Bass, San Francisco.

Coleman, Peter T., 2011. The Five Percent: Finding Solutions to Seemingly Impossible Conflicts. PublicAffairs, New York.

DeCaro, Daniel, Stokes, Michael, 2008. Social-psychological principles of community-based conservation and conservancy motivation: attaining goals within an autonomy-supportive environment. Conserv. Biol. 22 (6), 1443–1451.

Deutsch, Morton, 1973. The Resolution of Conflict. Yale University Press, New Haven, CT.

Deutsch, M., Coleman, P.T., 2012. Psychological Components of Sustainable Peace. Springer, New York.

Deutsch, M., Coleman, P.T., Marcus, E.C., 2006. The Handbook of Conflict Resolution: Theory and Practice. Jossey-Bass, San Francisco, CA.

Dickman, A.J., 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. Anim. Conserv. 13 (5), 458–466.

Doucey, Marie, 2011. Understanding the root causes of conflicts: why it matters for international crisis management. Int. Aff. Rev. XX (2).

Dudley, Joseph P., Ginsberg, Joshua R., Plumptre, Andrew J., Hart, John A., Campos, Liliana C., 2002. Effects of war and civil strife on wildlife and wildlife habitats. Conserv. Biol. 16 (2), 319–329.

Dukes, E., 1999. Why conflict transformation matters: three cases. Peace Conflict Studies 6 (2), 47–66.

Ellis, C., Koziell, I., McQuinn, B., Stein, J., 2005. Approaching the table: transforming conservation-community conflict into opportunity. In: Beyond the Arch: Community and Conservation in Greater Yellowstone and East Africa. 7th Biennial Scientific Conference on the Greater Yellowstone Ecosystem. Proceedings edited by Alice Wondrak Biel. October 6–8, 2003, Yellowstone National Park, Mammoth Hot Springs.

Engelberg, Moshe, Kirby, Susan D., 2001. Identity building in social marketing. Social Market. Quart. 7 (2), 8–15.

Fisher, R., Ury, W., Patton, B., 1991. Getting to Yes: Negotiating Agreement Without Giving In. Houghton Mifflin Harcourt, Boston.

Frahm, Jennifer, Brown, Kerry, 2007. First steps: linking change communication to change receptivity. J. Organ. Change Manag. 20 (3), 370–387.

Galtung, J., 1990. International Development in Human Perspective. In: Burton, J.W. (Ed.), Conflict. St. Martin's Press, New York.

Gibbs, Carole, Gore, Meredith L., McGarrell, Edmund F., Rivers, Louie, 2010. Introducing conservation criminology towards interdisciplinary scholarship on environmental crimes and risks. British J. Criminol. 50 (1), 124–144.

Ginges, J., Atran, S., Medlin, D., Shikaki, K., 2007. Sacred bounds on rational resolution of violent political conflict. In: Proceedings of the National Academy of Sciences of the United States of America.

Global Coalition for Conflict Transformation, 2014. Principles of Conflict Transformation. <http://www.transconflict.com/gcct/principles-of-conflict-transformation/>.

Hanson, Thor, Brooks, Thomas M., Da Gustavo, A.B., Fonseca, Michael Hoffmann, Lamoreux, John F., Machlis, Gary., Mittermeier, Cristina G., Mittermeier, Russell A., Pilgrim, John D., 2009. Warfare in biodiversity hotspots. Conserv. Biol. 23 (3), 578–587.

Hendrick, Diane., 2009. Complexity Theory and Conflict Transformation: An Exploration of Potential and Implications. Centre for Conflict Resolution, Department of Peace Studies, Working Paper 17, June 2009, University of Bradford.

Hicks, Tim, 2001. Another look at identity-based conflict: the roots of conflict: the roots of conflict in the psychology of consciousness. Negotiation J. 17 (1), 35–45.

Human-Wildlife Conflict Collaboration (HWCC), 2008. Benefitting Conservation Through Conflict Transformation white paper, Washington, DC.

Jackson, R.L., Hillard, D., Wangchuk, R., 2001. Encouraging local participation in efforts to reduce livestock depredation by snow leopard and wolf in Ladakh, India. Carnivore Damage Prevention News 4, 2–6.

Jeong, Ho-Won, 2008. Understanding Conflict and Conflict Analysis. Sage Publications, London.

King, Lucy E., Douglas-Hamilton, Iain, Vollrath, Fritz, 2011. Beehive fences as effective deterrents for crop-raiding elephants: field trials in northern Kenya. Afr. J. Ecol..

Lachapelle, Paul, 2008. A sense of ownership in community development: understanding the potential for participation in community planning efforts. Commun. Develop. 39 (2), 52–59.

LeBaron, Michelle, Pillay, Venashri (Eds.), 2006. Conflict Across Cultures: A Unique Experience of Bridging Differences. Intercultural Press, London.

Lederach, J.P., 1997. Building Peace: Sustainable Reconciliation in Divided Societies. United States Institute for Peace.

Lederach, J.P. 2003. Little Book of Conflict Transformation, Good Books.

Lederach, John Paul, 2005. The Moral Imagination: The Art and Soul of Building Peace. Oxford University Press, Oxford, MA.

Lederach, J.P., Neufeldt, R., Culbertson, H., 2007. Reflective Peace building: A Planning, Monitoring and Learning Toolkit. The Joan B. Kroc Institute for International Peace Studies, University of Notre Dame and Catholic Relief Services.

Leong, Kirsten M., Forester, John F., Decker, Daniel J., 2009. Moving public participation beyond compliance: uncommon approaches to finding common ground. George Wright Forum 26 (3).

Leong, Kirsten M., Emmerson, David P., Byron, Rebecca (Rudi), 2011. The new governance era: implications for collaborative conservation and adaptive management in department of the interior agencies. Human Dimensions Wildlife 16, 236–243.

Levinger, Matthew., 2013. Conflict analysis: understanding causes, unlocking solutions. United States Institute of Peace Academy Guides. USIP Press, Washington, DC.

Lewandowski, Jill, 2015. Transforming wicked environmental problems in the government arena – a case study of anthropogenic noise and marine mammals. In: Draheim, Megan, Madden, Francine, McCarthy, Julie-Beth, Parsons, Chris (Eds.), Human-Wildlife Conflict: Complexity in the Marine Environment. Oxford University Press, Oxford.

Lovallo, D., Sibony, O., 2010. The Case for Behavioral Strategy. McKinsey, McKinsey Quarterly. Boston.

Madden, F., 2004. Creating coexistence between humans and wildlife: global perspectives on local efforts to address human-wildlife conflict. Human Dimensions Wildlife 9, 247–257.

Madden, F., Kenyon Marc, Riske Steve, Cullens Lynn, Gotliffe Amy, Parrot Joel, McDonald Zara, Craighead Kimberly, 2013. Transforming Stakeholder Conflict over Mountain Lions in California. Presentation at The Wildlife Society Conference. October 7, 2013. Milwaukee, WI.

Manolis, J.C., Chan, K.M., Finkelstein, M.E., Stephens, S., Nelson, C.R., Grant, J.B., Dombeck, M.P., 2009. Leadership: a new frontier in conservation science. Conserv. Biol. 23 (4), 879–886.

Marker, S., 2003. Unmet human needs. In: Burgess, G., Burgess, H. (Eds.), Beyond Intractability. Conflict Information Consortium. University of Colorado, Boulder.

Maslow, A., 1954. Motivation and Personality. Addison-Wesley Publishing Company, Reading.

Max-Neef, Manfred A., Elizalde, A., Hopenhayn, M., 1989. Human Scale Development: Conception, Application and Further Reflections. Apex, New York.

Miall, Hugh, 2004. Conflict transformation: a multi-dimensional task. In: Berghof Handbook for Conflict Transformation. Berghof Research Center for Constructive Conflict Management, Berlin.

Michalski, F., Boulhosa, R.L.P., Faria, A., Peres, C.A., 2006. Human–wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. Anim. Conserv. 9, 179–188.

Moore, C.W., 1986. The Mediation Process: Practical Strategies for Resolving Conflict. Wiley.

Musiani, Marco, Muhly, Tyler, Callaghan, Carolyn, Cormack Gates, C., Smith, Martin E., Stone, Suzanne, Tosoni, Elisabetta, 2004. Wolves in rural agricultural areas of western North America: conflict and conservation. In: Fascione, Nina, Delach, Aimee, Smith, Martin (Eds.), 2009, People and Predators: From Conflict to Coexistence. Island Press, Washington, DC.

Naughton-Treves, L., Grossberg, R., Treves, A., 2003. Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. Conserv. Biol. 17 (6), 1500–1511.

Nie, M.A., 2002. Wolf recovery and management as value-based political conflict. Ethics, Place Environ. 5, 65–71.

Nie, M.A., 2003. Beyond Wolves: The Politics of Wolf Recovery and Management. University of Minnesota Press.

Nie, M., 2004. State wildlife governance and wildlife conservation. In: Fascione, Nina, Delach, Aimee, Smith, Martin (Eds.), People and Predators: From Conflict to Coexistence. Island Press, Washington, DC.

Nyhus, Philip J., Osofsky, Steven A., Ferraro, Paul, Madden, Francine, Fischer, Hank, 2005. Bearing the costs of human-wildlife conflict: the challenges of compensation schemes. In: Woodroffe, Rosie, Thirgood, Simon, Rabinowitz, Alan (Eds.), People and Wildlife, Conflict or Coexistence? Cambridge University Press, Cambridge.

Osborn, Ferrel V., Parker, Guy E., 2003. Towards an integrated approach for reducing the conflict between elephants and people: a review of current research. Oryx 37 (01), 80–84.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Zander, K.K., Swanson, A., et al., 2013. Conserving large carnivores: dollars and fences. Ecol. Lett. 16 (5), 635–641.

Pearce, W. Barnett, Littlejohn, Stephen W., 1997. Moral Conflict: When Social Worlds Collide. Sage Inc., Thousand Oaks, CA.

Peterson, M.N., Peterson, M.J., Peterson, T.R., Leong, K., 2013. Why transforming biodiversity conservation conflict is essential and how to begin. Pacific Conserv. Biol. 19 (2), 94–103.

Ramsbotham, Oliver, Miall, Hugh, Woodhouse, Tom, 2011. Contemporary Conflict Resolution. Polity, Cambridge, UK.

Redpath, Steve M., Young, Juliette, Evely, Anna, Adams, William M., Sutherland, William J., Whitehouse, Andrew, Amar, Arjun, Lambert, Robert A., Linnell, John D.C., Watt, Allan, Gutiérrez, R.J., 2013. Understanding and managing conservation conflicts. Trends Ecol. Evol. 28 (2), 100–109.

Reed, M., 2008. Stakeholder participation for environmental management: a literature review. Biol. Conserv. 141, 2417–2431.

Reid, R.S., Nkedianye, D., Said, M.Y., Kaelo, D., Neselle, M., Makui, O., Onetu, L., Kiruswa, S., Ole Kamuaro, N., Kristjanson, P., Ogutu, J., BurnSilver, S.B., Goldman, M.J., Boone, R.B., Galvin, K.A., Dickson, N.M., Clark, W.C., 2009. Evolution of models to support community and policy action with science: balancing pastoral livelihoods and wildlife conservation in savannas of East Africa. In: Proceedings of the National Academy of Sciences of the United States of America.

Ring, R. 2011. Rocky Mountain wolf recovery leader was not your average bureaucrat. High Country News. July 18.

Rothman, J., 1997. Resolving identity-based conflict. In: Nations, Organizations, and Communities. Jossey-Bass Publishers, San Francisco.

Rudolph, Brent A., Schecter, M.G., Riley, S.J., 2012. Governance of wildlife resources. In: Decker, Daniel J., Riley, Shawn J., Siemer, William F. (Eds.), Human Dimensions of Wildlife Management. Johns Hopkins University Press, Baltimore, MD.

Satterfield, Terre, 2002. Anatomy of a Conflict: Identity, Knowledge, and Emotion in Old-growth Forests. University of British Columbia Press, Vancouver, BC.

Senge, Peter M., 1997. The fifth discipline. Measuring Business Excellence 1 (3), 46–51.

Simon, A., 2013. A historical and case study analysis of the reasons why many trophy hunters are hostile toward wolves and wolf advocates. Capitalism Nature Socialism 24 (1), 104–120.

Sitati, Noah W., Walpole, Matthew J., 2006. Assessing farm-based measures for mitigating human-elephant conflict in Transmara District, Kenya. Oryx 40, 279–286.

Sites, P., 1990. Needs as analogues of emotions. In: Burton, J.W. (Ed.), Conflict: Human Needs Theory. St. Martin's Press, New York.

Smith, Keith L., Torppa, Cynthia B., 2010. Creating the capacity for organizational change: personnel participation and receptivity to change. J. Extension 48 (4).

Songhurst, Anna (Ed.). 2010. Working towards coordinated regional approaches in human-elephant conflict management. In: Proceedings of a Workshop for the Kwando-Kavango Region Organized by Conservation International. Maun, Botswana.

Treves, Adrian, Wallace, R.B., White, S., 2009. Participatory planning of interventions to mitigate human-wildlife conflict. Conserv. Biol. 23 (6), 1577–1587.

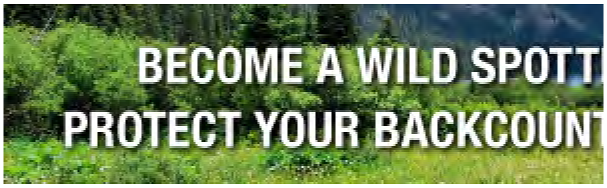
Walker, G., Daniels, S., 1997. Foundations of natural resource conflict: conflict theory and public policy. In: Solberg, B., Miina, S. (Eds.). Conflict Management and Public Participation in Land Management. EFI Proceedings 14, European Forest Institute.

Wellsmith, Melanie, 2011. Wildlife crime: the problems of enforcement. Eur. J. Crim. Policy Res. 17 (2), 125–148.

Wheatley, Margaret, 1998. The promise and paradox of community. In: Hesselbein, Frances, Goldsmith, Marshall, Beckhard, Richard, Schubert, Richard F. (Eds.), The Community of the Future. The Peter Drucker Foundation for Nonprofit Management, New York.

Woodroffe, Rosie, Thirgood, Simon, Rabinowitz, Alan (Eds.), 2005. People and Wildlife, Conflict or Coexistence? Cambridge University Press, Cambridge.

Zimmermann, Alexandra, Davies, Tammy E., Hazarika, Nandita, Wilson, Scott, Chakrabarty, Joydeep, Hazarika, Bhaben, Das, Dhruba, 2009. Community-based human-elephant conflict management in assam. Gajaha J. Asian Elephant Spec. Group 30, 41–52.



WILDLIFE

Varmint hunters sidelined in Wyoming

The Forest Service takes a stand for prairie dogs

Mark Matthews | July 2, 2001 | *From the print edition* |

PRINT

Mary Peterson doesn't regard the black-tailed prairie dog as a warm, fuzzy creature. The supervisor of southern Wyoming's Medicine Bow-Routt National Forest knows that many ranchers in the Great Plains look upon the animal as a pest that eats grass intended for cows. But she also recognizes that prairie dog burrows shelter numerous other critters, and many of those squatters like to eat the chubby rodents.

This spring, Peterson curtailed the sport shooting of prairie dogs at Thunder Basin National Grassland in eastern Wyoming; the area contains one of only seven large black-tailed prairie dog complexes remaining in North America.

"The Forest Service is responsible for trying to maintain biodiversity on its public lands, and I want to fulfill my obligation to preserve all special habitats," Peterson says.

The move, which bans shooting on 72,500 acres of grassland, is one of a growing number of actions being taken on behalf of the beleaguered prairie dog. The U.S. Fish and Wildlife Service has identified the rodent as a candidate species for listing under the Endangered Species Act, but the agency says it doesn't have the funding or resources to manage it right now. Consequently, 11 Western states are scrambling to come up with their own conservation plans to sidestep more sweeping ESA restrictions (HCN, 8/16/99: Standing up for the underdog)

The Forest Service, led by Peterson, has been the most proactive federal agency. While supervisor of Nebraska National Forest, Peterson in 1999 shut down shooting on a portion of the Buffalo Gap National Grasslands on the western border of Nebraska and South Dakota. The goal was to protect the extremely rare black-footed ferret, which lives in prairie dog burrows and dines almost exclusively on prairie dogs. Biologists released ferrets at Buffalo Gap in 1995, and today about 200 inhabit the area.

Ferrets are also destined for Thunder Basin, which has even more prairie dogs. For Peterson, the shooting ban was a logical step: She wants to make sure there are still plenty of prairie dogs around when federal biologists release the foot-long, weasel-like predators, most likely in 2002. She says she was concerned by the large number of shooters who have been eyeing Thunder Basin in the wake of restrictions in Colorado and South Dakota.

"The number of requests for information about shooting at Thunder Basin have increased exponentially since January," she says.

But barring sharpshooters can be a complicated affair. For one, it riles people up. "I don't see how that (Thunder Basin closure) is going to do anything," says Chuck Cornett, editor of Prairie Dog Digest, a publication dedicated to prairie dog hunting. "There are plenty of prairie dogs there."

Shooting bans also highlight jurisdictional problems. Individual states manage wildlife, while the federal agencies control much of the land on which those animals exist. Peterson had to find a way of prohibiting the killing of prairie dogs without stepping on the toes of Wyoming bureaucrats.

"They were okay with wording that prohibited the discharge of firearms in the area as long as it didn't affect turkey or antelope hunting seasons," she says. The ban puts prairie dogs off-limits from May through September.

Environmentalists applaud Peterson's action, but note that other federal and state agencies have moved slower than the Forest Service. In Montana, the Bureau of Land Management has banned shooting on 15 [illegible] dog towns, all less than 100 acres in size, in south Phillips County. But that's not enough, says Jonathan Proctor of the Bozeman, Mont.-based Predator Conservation Alliance.

"For ferret reintroduction to be successful, the BLM must protect all the prairie dog towns within their own designated ferret recovery area. Not just protect them from shooting, but also translocate animals to jump-start new towns," he says.

But the BLM says it's waiting for the state to finish its conservation plan before taking action. The state is closing in on its final prairie dog plan, and new shooting restrictions will likely be part of it, says Dennis Flath, Montana's nongame species coordinator. The state also plans to translocate prairie dogs, "but only to areas where it lived before," he says.

Proctor says Montana's preparations shouldn't take the BLM off the hook this year. "The BLM and state have been trying to pass the buck to each other for the last six years," he says.

Shooters are also tiring of the politics surrounding the creature. Cornett, a resident of Fresno, Calif., organizes an annual prairie dog shoot for a dozen writers and 65 shooters. This July, his party will travel to Montana's Fort Belknap Indian Reservation, which straddles Blaine and Phillips counties. Prairie dog shooters are still welcomed there.

Mark Matthews writes from Missoula, Montana.

YOU CAN CONTACT ...

- Jon Silvius, Medicine Bow-Routt National Forest, 307/745-2408;
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The Prairie Dog and Biotic Diversity

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Abstract: *Since the turn of this century, prairie dog populations have declined as much as 98% throughout North America, largely as a result of prairie dog eradication programs. The prairie dog is a keystone species that plays an important role in maintaining the biotic integrity of the western grasslands that stretch from southern Canada to northern Mexico. The fragmentation of prairie dog distribution has degraded diversity on those prairies, and several species depending on prairie dogs have achieved listing status under the Endangered Species Act. We propose that managing the prairie dog would provide an effective avenue from single-species management to management of a system. Because prairie dogs have declined so profoundly, some form of legal protection will be required. In addition, protected areas can preserve habitat and integrate ecologically sound agricultural opportunities. Positive incentives for ranchers to manage in the interests of both livestock and wildlife will enhance the attitude change necessary for grassland conservation. These management options hinge critically on an end to U.S. government subsidies for prairie dog eradication programs. The subsidies are financially and ecologically unsound, and they only contribute to the prevailing misconceptions about the role of the prairie dog on the grasslands.*

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El perro de las praderas y la diversidad biótica

Resumen: *Desde el comienzo de este siglo, los perros de las praderas han declinado hasta en un 98% a lo largo de América del Norte, principalmente como resultado de los programas de erradicación. El perro de las praderas es una especie clave que juega un rol importante en el mantenimiento de la integridad biótica de las praderas del oeste que se extienden desde el sur de Canada hasta el norte de México. La fragmentación de la distribución del perro de las praderas ha degradado la diversidad de esas praderas, y varias especies que dependen de los perros de las praderas han alcanzado el estatus para ser listadas bajo el Acta de Especies en Peligro. Nosotros proponemos que el manejo del perro de las praderas sería un medio efectivo para pasar de un manejo de especies particulares al manejo de un sistema. Dado que el perro de las praderas ha declinado en forma tan profunda, se necesitará algún tipo de protección legal. En forma adicional, las áreas protegidas pueden preservar el hábitat e integrar oportunidades agrícolas buenas desde un punto de vista ecológico. Incentivos positivos para los rancheros que manejan sus campos tratando de favorecer tanto el ganado como la vida salvaje mejorarán el cambio de actitud necesario para la conservación de las praderas. Estas opciones de manejo dependen en forma crítica del fin de los subsidios del gobierno de EEUU para los programas de erradicación de los perros de las praderas. El subsidio es financiera y ecológicamente insano y sólo contribuye al mantenimiento de las ideas erróneas que prevalecen acerca del rol de los perros de las praderas en las praderas.*

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Prairie Dog Distribution and Poisoning

At the beginning of this century, prairie dog (*Cynomys* spp.) colonies covered between 40 (Marsh 1984) and 100 million ha (Anderson et al. 1986) of native short- and mixed-grass prairies in western North America, but by 1960 that area had been reduced to about 600,000 ha (Marsh 1984). At the most conservative estimate, this represents a 98% decline for the five species of prairie dogs. A significant part of that reduction was the direct result of federal- and state-sponsored prairie dog control programs intended to benefit the U.S. livestock industry (Miller et al. 1990).

Merriam (1902) once estimated that prairie dogs reduced range productivity 50–75%. Subsequently, millions of acres were poisoned (Bell 1921; Day & Nelson 1929; Anderson et al. 1986; Dunlap 1988). Those programs continue today. Between 1980 and 1984, the Pine Ridge Reservation eradicated 185,600 ha of prairie dogs at a cost of $6,200,000 U.S. (Hanson 1988; Sharps 1988). Between 1986 and 1987, South Dakota destroyed the largest remaining black-tailed prairie dog (*Cynomys ludovicianus*) complex (110,000 ha) in North America (Tschetter 1988). Recently, a large area of northeastern Colorado was approved for poisoning (U.S. Fish and Wildlife Service 1991). U.S. public lands, including several National Parks, are poisoned (Schenbeck 1986), even though less than 5% of the U.S. beef weight is produced on federally owned lands (U.S. General Accounting Office 1988). In total, the Environmental Protection Agency and the Animal Plant Health Inspection Service (the present name for the federal Animal Damage Control unit) estimated that 80,000 ha of prairie dogs are eliminated annually as a result of their permitting authority and activities (Captive Breeding Specialist Group 1992).

Eradication programs continue despite modern research showing only a 4–7% level of competition between livestock and prairie dogs; in other words, about 300 prairie dogs eat as much as one cow with a calf (Uresk & Paulson 1988). Other studies have reported no significant difference in market weight whether or not steers lived with prairie dogs (Hansen & Gold 1977; O'Meilia et al. 1982). Indeed, throughout history prairie dogs coexisted harmoniously with hundreds of millions of bison (*Bison bison*), elk (*Cervus elaphus*), and pronghorn antelope (*Antilocapra americana*); these ungulates, as well as domestic cattle, prefer to graze on prairie dog towns, where the grass is more succulent and nutritious (Coppock et al. 1983; Wydeven & Dahlgren 1985; Krueger 1986; Knowles 1986; Detling & Whicker 1988).

It is not surprising that a cost-benefit analysis indicated a net financial loss in poisoning efforts (Collins et al. 1984), and that analysis was conservative. It did not consider the long-term expenses of recovering a degraded ecosystem, the intangible value of biological diversity as a public benefit, or the loss of potential or actual wealth from the depletion of biotic resources.

As a result of the poisoning programs, the few remaining prairie dog colonies are smaller and more isolated. These fragmented colonies are more susceptible to extirpation, particularly by sylvatic plague (*Yersinia pestis*). Yet some individuals argue that prairie dog populations are safe because prairie dogs can still be found throughout a geographical region between Canada and Mexico. That analysis masks the severity of habitat fragmentation. Fragmented habitat jeopardizes populations by several avenues: (1) demographic units are eliminated, reduced, or subdivided, increasing the probability of extinction by other means such as disease, genetic problems, demographic events, or natural catastrophes; (2) sources of immigration are lost; and (3) habitat alteration between occupied colonies obstructs recolonization or genetic exchange (Wilcox & Murphy 1985). As a result of these factors, the risk of extinction from habitat disruption is not linearly proportional to the reduction of habitat, but in fact may increase disproportionately (Wilcox & Murphy 1985; Wilcove et al. 1986).

In some cases, reductions of one species may cause a wave of secondary extinctions that affects species diversity (Wilcox & Murphy 1985; Wilcove et al. 1986). The five species of prairie dog are all considered keystone species, and the loss of prairie dog populations is threatening vertebrate biodiversity in the prairie ecosystem (Koford 1958; Clark et al. 1989; Reading et al. 1989; Miller et al. 1990; Sharps & Uresk 1990). Compared to surrounding grasslands without prairie dogs, the prairie dog ecosystem supports higher numbers of small mammals and arthropods, more terrestrial predators, higher avian species diversity, and higher avian density (Hansen & Gold 1977; O'Meilia et al. 1982; Agnew et al. 1986; Krueger 1986; Reading et al. 1989). Approximately 170 vertebrate species rely at some level on prairie dog activity for survival (Reading 1993), and the presence of prairie dogs favors plant diversity and increases grasses and forbs grazed by livestock and big game (Bonham & Lerwick 1976). So the five species of prairie dog, through their burrowing and grazing activities, are ecosystem regulators that augment primary productivity, species densities, species diversity, soil structure, and soil chemistry (Sieg 1988; Detling & Whicker 1988; Reading et al. 1989).

Highly specialized animals are most vulnerable to the negative effects of habitat fragmentation. For example, the eradication of prairie dogs has caused the near extinction of black-footed ferrets (*Mustela nigripes*). Recently, Mountain Plovers (*Charadrius montanus*), Ferruginous Hawks (*Buteo regalis*), and swift foxes (*Vulpes velox*) have been proposed as candidate species under the U.S. Endangered Species Act, and their listing proposals cited prairie dog poisoning as a factor in their decline. Mountain Plovers require open, short-grass nesting sites, so prairie dogs are particularly important to their nesting requirements in areas where sagebrush is present. In addition, Ferruginous Hawks and swift foxes exploit the abundant prey resources of the prairie dog colonies. Because the poisoning continues, other species that rely on prairie dogs will eventually need federal aid for survival. The term "ecological trainwreck" could soon be a reality on the western prairies.

Managing Conflict and Biodiversity on the Grasslands

Past methods of reducing conflict between livestock interests and prairie dogs have failed. As a result, the western Great Plains have lost biodiversity, and managers are spending increasing amounts of money and time to rescue species that depend on prairie dogs.

Historically, managing each threatened species individually served a useful purpose in slowing the decline toward extinction. During the early years of environmental action, there were already a number of species in a crisis situation, and single-species management was necessary to prevent further loss. Recently, however, legal experts and biologists have advocated moving from the single-species approach toward managing entire systems of species (e.g. Smith 1984; Scott et al. 1987; Rohlf 1991). We propose a solution that combines legal protection, habitat preservation, conservation incentives, and education into an integrated approach toward conservation of the prairie dog ecosystem.

(1) *Legal Intervention via the Endangered Species Act.* As a keystone species, the prairie dog provides an excellent opportunity to forge a gradual transition from historical single-species management to management of a system. It would be preferable to manage the keystone species proactively before legal intervention is necessary. However, prairie dog populations have already declined too severely to avoid legal recognition, particularly with the causes of decline still active (prairie dog poisoning programs and sylvatic plague). The Endangered Species Act can play an enormous role in broad-scale preservation of biodiversity by protecting keystone species and, therefore, all species that are in some way dependent on them (Rohlf 1991).

Protecting a threatened keystone species would provide educational, biological, and fiscal benefits. By protecting a keystone species such as the prairie dog, the public could be educated about the value of ecosystem conservation and the links between animals and their habitat. The transition from species to system would be straightforward because the keystone species controls a system. Biologically, the ecological integrity of the western prairie grasslands would quickly benefit from the protection afforded the prairie dog. Fiscally, governments would be spared the financial burden of maintaining an expensive support system for other species that will become imperiled as the prairie dog continues to decline. The captive breeding and reintroduction program for the black-footed ferret cost $1,524,870 U.S. in 1991 alone (U.S. Fish and Wildlife Service 1992). Because there was only one reintroduction site in 1991, that total is certain to rise as the program expands.

Protection of the keystone species, no matter how political the situation, would be far more cost-effective than trying to protect each individual species that depends upon it. This is particularly true for the prairie dog. The U.S. government financially subsidizes both the poisoning of the prairie dog and the preservation of species that depend on the prairie dog for survival.

(2) *Habitat.* Conservation of most species, however, depends on more than legal action. Many species are protected by law, but enforcement in the field can sometimes be difficult, and legal maneuvers can circumvent the intentions of most endangered species legislation (Salwasser 1990). In addition, legal efforts alone often create unproductive conflict.

The value of creating protected areas on the grasslands of Canada, the United States, and Mexico can not be overemphasized. There are presently plans to initiate such a protected area in northern Chihuahua, Mexico, that would include a 55,000-ha black-tailed prairie dog complex, which is the largest remaining in North America (Ceballos et al. 1993).

Establishing areas of protected habitat could prevent the further decline of the prairie dog and of the many life forms that depend on its system, as well as integrate ecologically sound agricultural opportunities with conservation goals. This proactive integration would be a large step toward elimination of the conflict that arise when a species is on the verge of extinction (as with the Northern Spotted Owl).

(3) *Education and Positive Incentives.* Protected area alone are not sufficient to preserve most declining species. Size constraints combined with the effects of fragmentation often do not permit viable populations large or highly specialized species (Ceballos & Navarr 1991). An alternative to the conflicting directives federally sponsored prairie dog poisoning and endangered species management has been proposed. This program is designed to restore ecological integrity witho harming local livestock interests (Miller et al. 1990 The proposal basically converts federal funds allocat to the destruction of prairie dogs into a positive ince tive for ranchers who manage for both livestock a wildlife.

Because attitudes of the western agricultural comm nity are entrenched on the issue of prairie dogs, it will take a positive incentive before education can work. In Montana, Reading and Kellert (1993) showed that knowledge was only one part of attitude and that different levels of knowledge alone did not change negative perceptions about black-footed ferrets and prairie dogs.

It is not possible for education to address misconceptions about the prairie dog ecosystem when poisoning is still federally subsidized. Words may say one thing, but actions quickly override their content. As long as the U.S. government provides poison, ranchers will use it, and their misconceptions about the role of the prairie dog in grassland maintenance will only be reinforced instead of changed. To continue this subsidy, and the present poisoning policies, will undermine all efforts to conserve biological diversity on the western grasslands.

Conclusion

Without addressing the issues surrounding the destruction of the prairie dog, we will only continue to degrade the western grasslands, reduce biotic diversity, and drain government budgets. Protection of this keystone species will provide the best transition from single-species management to management of all animals and plants depending on the system. Because the prairie dog ecosystem stretches across three North American countries, the responsibility for preservation of its unique lifeforms must be a coordinated international effort. The Great Plains Initiative is one recent document that provides an avenue for this cooperation, and we should seize the opportunity. The conservation of biotic diversity in this hemisphere cannot afford less.

Literature Cited

Agnew, W., D. W. Uresk, and R. M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed grass prairie in western South Dakota. Journal of Range Management 39:135–139.

Anderson, E., S. C. Forrest, T. W. Clark, and L. Richardson. 1986. Palio-biology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851. Great Basin Naturalist Memoirs 8:11–62.

Bell, W. R. 1921. Death to the rodents. U.S. Department of Agriculture Yearbook 1920:421–438.

Bonham, C. D., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. Journal of Range Management 29:221–225.

Captive Breeding Specialist Group. 1992. Black-footed ferret recovery plan review, Washington D.C. July 22–24. Captive Breeding Specialist Group, Apple Valley, Minnesota.

Ceballos, G., and D. Navarro. 1991. Diversity and conservation of Mexican mammals. Pages 167–198 in M. A. Mares and D. J. Schmidly, editors. Topics in Latin American mammals: Ecology, evolution, and education. University of Oklahoma Press, Norman, Oklahoma.

Ceballos, G., E. Mellink, and L. R. Hanebury. 1993. Distribution and conservation status of prairie dogs (*Cynomys mexicanus*) and *Cynomys ludovicianus* in Mexico. Biological Conservation 63:105–112.

Clark, T. W., D. Hinckley, and T. Rich, editors. 1989. The prairie dog ecosystem: Managing for biodiversity. Technical Bulletin 2. Montana Bureau of Land Management Wildlife, Billings, Montana.

Collins, A. R., J. P. Workman, and D. W. Uresk. 1984. An economic analysis of the black-tailed prairie dog (*Cynomys ludovicianus*) control. Journal of Range Management 37:358–361.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983. Plant herbivore interactions in a mixed grass prairie: I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1–9.

Day, A. M., and A. P. Nelson. 1929. Wildlife conservation and control in Wyoming under the leadership of the United States Biological Survey. U.S. Biological Survey, Wyoming Game and Fish Department, Wyoming Department of Agriculture, Cheyenne, Wyoming.

Detling, J. K., and A. D. Whicker. 1988. A control of ecosystem processes by prairie dogs and other grassland herbivores. Pages 23–29 in Proceedings of the eighth Great Plains wildlife damage control workshop, Rapid City, South Dakota. U.S. Forest Service, Washington D.C.

Dunlap, T. R. 1988. Saving America's wildlife. Princeton University Press, Princeton, New Jersey.

Hansen, R. M., and I. K. Gold. 1977. Black-tailed prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. Journal of Range Management 30:210–214.

Hanson, R. 1988. A chronology of prairie dog control operations and related developments in South Dakota. Pages 121–122 in Proceedings of the Eighth Great Plains wildlife damage control workshop proceedings, Rapid City, South Dakota. U.S. Forest Service, Washington, D.C.

Knowles, C. 1986. Some relationships of black-tailed prairie dogs to livestock grazing. Great Basin Naturalist 46:198–203.

Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monograph 3:1–78.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: An experimental analysis. Ecology 67:760–770.

Marsh, R. E. 1984. Ground squirrels, prairie dogs and marmots as pests on rangeland. Pages 195–208 in Proceedings of the conference for organization and practice of vertebrate pest control, Hampshire, England, August 30–September 3, 1982. Plant Protection Division, Fernherst, England

Merriam, C. H. 1902. The prairie dog of the Great Plains. Pages 257–270 in Yearbook of the U.S. Department of Agriculture 1901. U.S. Government Printing Office, Washington, D.C.

Miller, B., C. Wemmer, D. Biggins, and R. Reading. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. Environmental Management 14:763–769.

O'Meilia, M. E., F. L. Knopf, and J. C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management 35:580–585.

Reading, R. P. 1993. Toward an endangered species reintroduction paradigm: A case study of the black-footed ferret. Ph.D. dissertation. Yale University, New Haven, Connecticut.

Reading, R. P., and S. Kellert. 1993. Attitudes toward a proposed reintroduction of black-footed ferrets (*Mustela nigripes*). Conservation Biology 7:569–580.

Reading, R. P., J. J. Grenston, S. R. Beissinger, and T. W. Clark. 1989. Attributes of black-tailed prairie dog colonies in north-central Montana, with management recommendations for the conservation of biodiversity. Pages 13–28 in T. W. Clark, D. Hinckley, and T. Rich, editors. The prairie dog ecosystem: Managing for biodiversity. Wildlife Technical Bulletin 2. Montana Bureau of Land Management, Billings, Montana.

Rolhf, D. J. 1991. Six biological reasons why the Endangered Species Act doesn't work—and what to do about it. Conservation Biology 5:273–282.

Salwasser, H. 1990. Sustainability as a conservation paradigm. Conservation Biology 4:213–216.

Schenbeck, G. L. 1986. Black-tailed prairie dog management on the northern Great Plains: New challenges and opportunities. Pages 28–33 in Proceedings of the Great Plains wildlife damage control workshop, vol. 7. Agriculture Communications, College Station, Texas.

Scott, J. M., B. Csuti, J. D. Jacobi, and J. Estes. 1987. Species richness: A geographical approach to protecting future biodiversity. Bioscience 37:782–788.

Sharps, J. 1988. Politics, prairie dogs, and the sportsman. Pages 117–118 in Eighth Great Plains Wildlife Damage Control Workshop Proceedings, April 28–30, 1987. Rapid City, South Dakota USDA Forest Service, Washington, D.C.

Sharps, J., and D. Uresk. 1990. Ecological review of black-tailed prairie dogs and associated species in western south Dakota. Great Basin Naturalist 50:339–345.

Sieg, C. H. 1988. Small mammals: Pests or vital components of the ecosystem. Pages 123–124 in Proceedings of the eighth Great Plains wildlife damage control workshop proceedings, vol. 9. U.S. Forest Service, Washington, D.C.

Smith, E. M. 1984. The Endangered Species Act and biological conservation. Southern California Law Review 57:361–413.

Tschetter, B. J. 1988. Estimates of South Dakota prairie dog acreages, 1987. Report No. 88.01 (unpublished). Department of Game, Fish, and Parks, Pierre, South Dakota.

U.S. Fish and Wildlife Service. 1991. Black-footed ferret habitat evaluation and search in northeastern Colorado. Final Report, December 27, 1991. U.S. Fish and Wildlife Enhancement, Golden, Colorado.

U.S. Fish and Wildlife Service. 1992. Federal and state endangered species expenditures for fiscal year 1991. U.S. Fish and Wildlife Service, Washington, D.C.

U.S. General Accounting Office. 1988. More emphasis needed on declining and overstocked grazing allotments. GAO/RCED-88-80. U.S. General Accounting Office, Washington, D.C.

Uresk, D. W., and D. B. Paulson. 1988. Estimated carrying capacity for cattle competing with prairie dogs and forage utilization in western South Dakota. Pages 387–390 in Symposium on management of amphibians, reptiles, and small mammals in North America, Flagstaff, Arizona, July 19–21, 1988. GTR RM-166. U.S. Forest Service, Washington, D.C.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, editor. Conservation biology. Sinauer Associates, Sunderland, Massachusetts.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: The effects of fragmentation on extinction. American Naturalist 125:879–887.

Wydeven, A. P., and R. B. Dahlgren. 1985. Ungulate habitat relationships in Wind Cave National Park. Journal of Wildlife Management 49:805–813.

Note Added in Proof

Since this article was written, the U.S. Fish and Wildlife Service, Region 6, has rejected an internal petition to list the black-tailed prairie dog as a candidate species. In our opinion this is very unfortunate for two reasons. (1) Prairie dogs have declined precipitously throughout this century and the causes of the decline (poisoning programs and plague) are still active. Candidate status would have focused attention and money on the problem and, because of the prairie dog's reproductive potential, candidate status may have reversed the downward trend in biodiversity without the restrictions o full endangered status. (2) The Department of Interio has been trumpeting a need to manage ecosystems instead of individual species. As a keystone species, candidate status for the prairie dog would have been a excellent step in that direction, but it appears that th U.S. Fish and Wildlife Service has chosen instead to li species individually that depend on prairie dogs and n recognize the root cause of lost biodiversity. We unde stand that there is tremendous political pressure fro the agricultural community on this issue, yet the histo ical alternatives have so far done little to alter the b logical trend or the attitudes behind it. We may be hea ing directly toward the "ecological train wreck" on t prairie that the Department of Interior says it wants avoid.

United States
Department of
Agriculture
Forest Service

**Rocky Mountain
Forest and Range
Experiment Station**

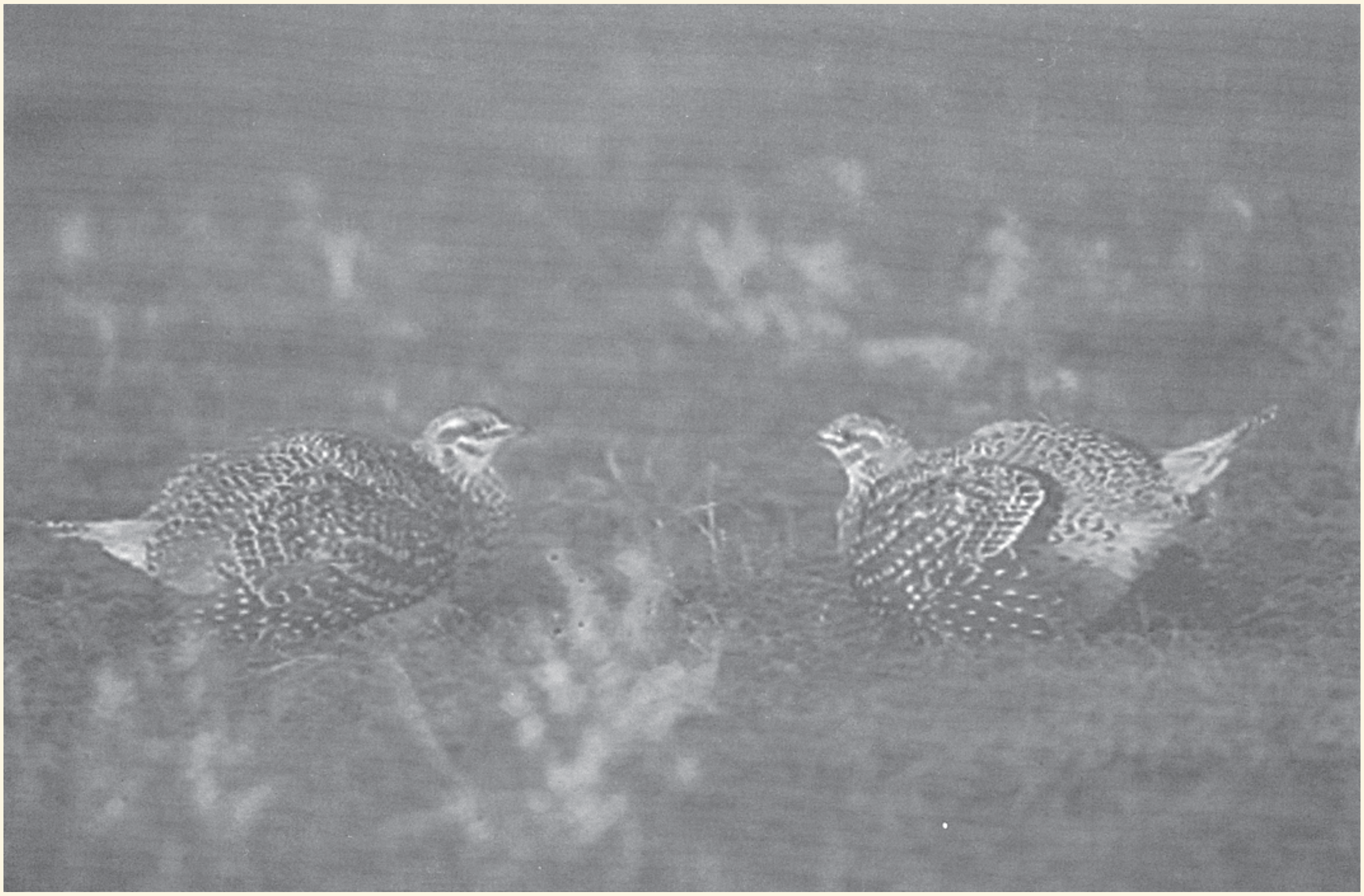
Fort Collins
Colorado 80526

**General Technical
Report RM-GTR-298**

Conserving Biodiversity on Native Rangelands: Symposium Proceedings

August 17, 1995

Fort Robinson State Park, Nebraska



Uresk, Daniel W.; Greg L. Schenbeck; James T. O'Rourke, tech coords. 1996. Conserving biodiversity on native rangelands: symposium proceedings; August 17, 1995; Fort Robinson State Park, Nebraska. General Technical Report RM-GTR-298. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 38 p.

Abstract: These proceedings are the result of a symposium, "Conserving biodiversity on native rangelands" held on August 17, 1995 in Fort Robinson State Park, NE. The purpose of this symposium was to provide a forum to discuss how elements of rangeland biodiversity are being conserved today. We asked, "How resilient and sustainable are rangeland systems to the increasing demands of a growing human population and to extended periods of drought?" Key programs and issues, identified by a program committee, were addressed by researchers and managers. Their papers provide research results, management findings, and describe management programs currently used to conserve rangeland biodiversity.

Keywords: biodiversity, rangeland, sustainability, drought, conservation

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USDA Forest Service
General Technical Report RM-GTR-298

September 1997

Conserving Biodiversity on Native Rangelands: Symposium Proceedings

August 17, 1995

Fort Robinson State Park, Nebraska

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Central Mountains and Plains Section of The Wildlife Society
Nebraska Chapter of The Wildlife Society

Contents

Introduction

Rangelands embody biological diversity of profound ecological and social significance, yet it is the biological diversity of forests and wetlands that has been the focus of research by scientists and concern by the public. Recently, a broad array of people, from ecologists and biologists to ranchers and recreationists, have begun to realize the importance of rangeland conservation and biological diversity. Although these groups may not always share a common vision of rangelands, they share a common interest in the land that will foster a better understanding and appreciation of the value of diverse and healthy rangelands.

Ranchers have long practiced conservation of rangeland biological diversity. Most recognize the importance of both warm and cool season grasses to round out their forage programs, and many have noticed that in some years one grass will do poorly while another will thrive, thus balancing the production. Ranchers depend on native grasses coming back on their own after drought or a bad grasshopper year; some species will return quicker than others. Looking toward the future, ranchers manage their grass for a diverse rangeland community, not a monotypic one. This is conservation of rangeland biological diversity at the grass roots level.

Together, scientists and rangeland managers are traveling to new levels of conservation of rangeland biodiversity, but the journey has some formidable challenges. Herbivory, fire, drought, and other natural events and processes historically shaped rangeland biodiversity and ecological processes long before human action. However, human influence on the range has complicated and interrupted many naturally occurring mechanisms. The use and control of fire has altered its frequency and intensity. The pattern, frequency, and intensity of herbivory by large animals has been modified by the conversion from free-ranging bison and other large ungulates to confined domestic livestock and a proliferation of livestock water developments. Cultivation has fragmented and isolated rangelands and often natural processes no longer function. An insidious challenge to rangeland biodiversity is the invasion of exotic plants into native range often at the expense of native biota.

The purpose of this symposium was to provide a forum to discuss how elements of rangeland biodiversity are being conserved today. We asked, “How resilient and sustainable are rangeland systems to the increasing demands of a growing human population and to extended periods of drought?” One way to begin answering this question is to look at our successes and failures in conserving all parts of rangeland systems. Key programs and issues, identified by a program committee, were addressed by researchers and managers. Their papers, which have received statistical and peer review, are presented here and provide research results, management findings, and describe management programs currently used to conserve rangeland biodiversity. The paper “Gap Analysis in the Great Plains: A Large-Scale Geographic Strategy for Conservation of Biodiversity” by Dennis Jelinski, Michael Jennings, and James Merchant was withdrawn by the authors before publication of this workshop proceedings.

This symposium was held concurrently with the Annual Meeting of the Central Mountains and Plains Section of The Wildlife Society. We thank the organizers of that event for suggesting this symposium. Thanks are also extended for the well-attended field trip to review northern swift fox management in southwestern South Dakota that concluded the workshop.

A Neotropical Migratory Bird Prioritization for National Forests and Grasslands

Dick Roth[1] **and Richard Peterson**[2]

Abstract.-The Rocky Mountain Region of the USDA Forest Service provides nesting habitat for 146 species of neotropical migratory birds. Interactive, prioritization databases were developed for each National Forest and National Grassland in the Region to assist land managers in making informed decisions about resource allocations. The data was processed using Paradox software. This paper summarizes the uses and application of the database for the Oglala and Ft. Pierre National Grasslands.

METHODS

We used data provided by Colorado Bird Observatory and ranked according to the Partners-In-Flight (PIF) ranking scheme for initial prioritization of neotropical migratory birds (NTMBs). The approach ranks species by their relative susceptibility to extinction (Carter and Barker 1993, Hunter et al. 1993). There are many factors that contribute to extinction probability. The PIF prioritization scheme uses seven criteria as the most important in gauging a species susceptibility to extirpation or extinction: 1) importance of area of consideration (IA), (percentage of a species range that is within a state or geographic area under consideration); 2) global abundance (GA); 3) the degree of threat to the species' persistence on the breeding ground (TB); 4) the degree of threat to species' persistence on the wintering ground (TW); 5) breeding distribution (BD); 6) extent of wintering distribution (WD); 7) population trend in area of consideration (PT); based upon U.S. Fish and Wildlife Service Breeding Bird Survey (BBS) data. Each of the seven criteria is weighted equally. An individual species is assigned a score in each of the seven categories ranging from one (low concern) to five (high concern). Each species is ranked according to the average of the seven scores. The importance of area score (IA) was modified for our use to include a rank based upon the percentage of the area under consideration which meets breeding habitat requirements for a given species.

Uncertainty values are assigned to each species in conjunction withvalues assigned for threats to breeding (TBU) and wintering (TWU), and population trend (PTU). These uncertainty values reflect the extent of the available information for each of the associated criteria. They indicate the extent and location of gaps in our knowledge of neotropical migrant biology. These values help us differentiate between species withdefinite management concerns and those requiring additional monitoring or research in order to more clearly reflect their status.

Several criteria were modified for the Oglala and Ft. Pierre National Grasslands. Population trend (PT) and Population trend uncertainty scores were determined from USFWS Breeding Bird Survey (BBS) for the lo-year and 26-year scores. Data from physiorgraphic region 39 (Missouri Plateau-Unglaciated) were used for both grasslands. Other population trend data more specific to the area under consideration canbe used for these criteria if available. Threats to breeding habitat (TB) and Threats to breeding habitat uncertainty (TBU) criteria provided by PIF were used (Carter and Barker 1993). Additionally, known local threats were also considered such as reduction of prairie dog towns as a threat to burrowing owl habitat. In this case, a TB score of 5 was used because loss of prairie dog towns would result in eliminationof burrowing owl habitat (Peterson 1994).

Several methods have been developed to determine priorities for community based conservation (Millsap et al. 1990, Master 1991, Reed 1992). The technique developed by Partners in Flight is essentially one that ranks individual species first, and secondarily ranks habitats based on individual species scores grouped by habitat preference. This ranking can then be used to develop and justify community based conservation programs. The

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tion of breeding occurrence and habitat preference of neotropical migratory landbirds on the Oglala and Ft. Pierre Grasslands was made using local expertise.

The habitat types and conditions developed for the Grasslands and assigned to each species have three levels:

1) Appropriate habitat contains six major breeding bird habitat types. They include trees/woodlands, shrubs/shrublands, grass/grasslands, edge-tree/grass-shrub/grass, wetlands and special topographic structure.
2) Suitable habitat, in general, additional conditions are needed for appropriate habitat to be suitable breeding habitat for a given species. For grasslands, additional conditions could be related to a given height and density of grasses or forbs. For trees/woodland habitat, additional conditions could include deciduous trees, cavities or a multi-layered canopy.
3) Special conditions includes topographic structures such as cliffs and cutbanks, but also includes features such as riparian areas and prairie dog towns.

These habitat categories enable development of habitat ranking based on a species' use of a wide variety of habitat types and variables.

Coding used for habitats and special features is as follows:

Habitats T-(t)rees/woodlands, coni(f)erous, (d)ediduous, (o)ld growth, m(u)ltilayer canopy, and
(c)avities.
E-(e)dge, tree-grass/shrub-grass.
S-(s)hrubs, (b)ig sagebrush, (2) thorny shrubs-esp. plum,
G-(g)rass/grasslands-open areas-esp. s(h)ort and/or sparse, t(a)ll and/or de(n)se, mi(x)ed/mid.
W-(w)etlands/(w)ater-(1)riparian, (m)arsh/tall emergent, (3) wet meadow-tall grass/short emergent.
Specials s(P)ecial-top/structure-(4)cliffs/caves/ledges and cutbanks, (5)buildings/bridges/chimneys and bird houses, lands/bare shores.
s(p)ecial-other-(7)prairie dog towns, (i.e. burrows/bare ground/short grass and associated prey), forest fire locations-(B)urned areas, esp. large with tall snags, (9) cropland-esp alfalfa, (O)old crow/magpie nests.

The mix of numbers and letters used in the coding may appear to be confusing; however, familiarization with the application of those codes as displayed in the habitat columns of the accompanying tables reveals that they provide a logical fit.

RESULTS

The Oglala and Ft. Pierre National Grasslands support 79 and 68 species of neotropical migratory landbirds which regularly nest there, or a combined total of 84 regular nesters. These are listed in Appendix 1 and 2 along with all associated prioritization scores for the seven criteria and some of the associated uncertainty scores. Species with R10 or R26 ranks of 3.00 or greater should be given high priority for management considerations (Thompson et al. 1993). Analysis of the data reveals that 18 of the 84 species have a R10 or R26 rank of 3.00 or greater (Appendix 1 and 2). The R10 and R26rank scores along with importance of area, threats to breeding and breeding distribution scores help to provide a framework for setting management priorities. As an illustration, the chestnut-collard longspur has high and R26 rank scores but has an importance of area (IA) score of only 3.00.

Consequently, other species with higher IA scores should be given higher management priority. The two top ranked species on both grasslands (burrowing owl and ferruginous hawk) have a preference for short-grass prairie and prairie dog towns. Other species on these two grassland have a preference for tall and mixed-grass prairie. Consequently, management of the National Grassland units for a diversity of heights and would provide habitat for both species.

The database contains scores for each criterion, for each species, for each unit where they are likely to occur. It is important that the data for each unit be analyzed separately for more specific insights into the top priority species and habitat for each unit. For example, what is the importance of the habitat on the unit being analyzed for a given species. What are the threats to that habitat? What is the status and trend of that habitat?

This prioritization system reveals that the highest ranked habitat on the Oglala National Grassland is big sagebrush and that is based on one species (table 1). The next highest ranked habitat is short and mixed-grass prairie and prairie dog towns respectively. These habitats support six and four high priority (= > 3) species respectively. Edge habitat and riparian habitat are both important because of the diversity of species that they support. These values are based upon the relative susceptibility to extinction of species found in each habitat. Information on species as presented in table 2 should also be considered along with the habitat information when weighing the consequences of management actions.

A total of 12 species from the Oglala National Grassland have a R26 Rank of 3.00 or greater. Brewer's Sparrow is the species in big sagebrush habitat which causes the high habitat rank in table 1. The rank of 1 for importance of area score (IA) indicates that only a small portion of the Oglala National Grassland provides suitable breeding habitat for Brewer's Sparrows. The two top-ranked species use prairie dog towns and the top five species also short to mixed grass prairie habitats.Therefore, the highest priority habitats for NTMBs on the Oglala National Grassland should be those that support these species.

Table 1. Habitat association scores for the Oglala National Grassland based on R26 species ranks.

Habitat	≤3	<3 to 2	<1 .99	# Species	Average score	Total score
Short/Mix Grass	6	1	1	8	3.08	24.71
Prairie Dog Towns	4	2	1	7	2.94	20.57
Mix/tall Grass	2	7		9	2.81	29.00
Trees Deciduous	2	8	2	12	2.48	29.71
Shrub Big Sage	1			1	3.14	3.14
Shrub Dense		5		5	2.60	13.00
Edge	1	15	7	23	2.32	53.41
Water/marsh		7	4	11	2.18	24.00
Riparian	2	15	5	22	2.36	51.99

Table 2. Species on the Oglala National Grassland with 10R10 or R=≥3.00.

Species	Hab	IA	AB	TB	BD	*RIO*	R26
Burrowing Owl	Gh7	5	4	**5**	3	3.57	3.86
Long-billed Curlew	Gxh7	5	3	3	4	3.86	3.71
Chestnut-collared Longspur	Gxh	3	3	**3**	4	3.29	3.57
Lark Bunting	Gxhs	5	2	**3**	4	3.29	3.43
Ferruginous Hawk	Gxht7	3	4	**4**	3	3.29	3.29
Black-billed Cuckoo	Tds12	2	3	**4**	3	3.29	3.14
Bobolink*	Ga39	1	2	**4**	3	3.14	3.14
Brewer's Sparrow	Sb	1	2	**4**	3	3.00	3.14
Loggerhead Shrike	Es2	3	3	**4**	2	3.00	3.14
Dickcissel*	Ga9	1	2	**4**	3	2.86	3.00
Great Crested Flycatcher	Tdcl	1	2	**4**	3	3.00	3.00
Prairie Falcon	Gxh47	4	3	**3**	3	3.14	3.00

** Species found in the area but not confirmed nester on National Grassland.*

Similar analysis of the data for the Ft Pierre National Grassland reveals somewhat different results (table 3). Ft Pierre is in a higher precipitation area and has taller grasses and more deciduous trees than the Oglala National Grassland. Bird species diversity is greater across habitat types than on the Oglala National Grassland and mixed/tall grass habitat higher priority. The burrowing owl is the highest ranked species on both units (table 4). Dickcissel , bobolink, grasshopper sparrow, northern harrier and upland sandpiper had higher prioritization scores on the Ft. Pierre National Grassland. Management of prairie dog towns and short grass habitat should have some priority on Ft. Pierre, but management for mixed to tall grass habitat is of higher priority based on this analysis.

Table 3. Habitat association scores for the Ft. Pierre National Grassland based on R26 species ranks.

Habitat	≥3	>3 to 2	>1.99	# Species	Average score	Total score
Short/Mix Grass	5	1	1	7	3.06	21.43
Prairie Dog Towns	3	2	1	6	2.81	16.86
Mix/Tall Grass	5	5		10	3.13	31.29
Trees Deciduous	2	9	2	13	2.50	32.58
Shrub Dense	1	5		6	2.26	13.57
Edge	1	9	7	17	1.98	33.70
Water/marsh	1	8	5	14	2.01	28.13
Riparian	3	14	5	22	2.39	52.58

Table 4. Species on Ft. Pierre National Grassland with RIO **or** R26 **scores ≥** 3.00.

Species	Hab	IA	TB	BD	AB	R10	R26
Burrowing Owl	Gh7	4	5	3	5	3.57	3.86
Baird's Sparrow*(Historic)	Gx3	4	5	5	0	3.86	3.71
Chestnut-collared Longspur	Gxh	3	3	4	3	3.29	3.57
Dickcissel	Ga9	2	3	3	5	3.29	3.43
Ferruginous Hawk	Gxht7	4	4	3	4	3.43	3.43
Lark Bunting	Gxhs	2	3	4	5	3.29	3.43
Bobolink	Ga39	2	3	3	3	3.29	3.29
Long-billed Curlew*	Gxh7	3	4	4	1	3.43	3.29
Bell's Vireo*	Sn12	3	4	3	1	3.14	3.14
Black-billed Cuckoo	Tdsl2	3	4	3	2	3.29	3.14
Grasshopper Sparrow	Gxa	2	2	2	5	2.57	3.00
Great Chrested Flycatcher*	Tdcl	2	4	3	1	3.00	3.00
Loggerhead Shrike	Es2	3	4	2	2	2.86	3.00
Northern Harrier	Gasm	3	3	1	5	3.00	3.00
Sprague's Pipit*(historic)	Gxa	3	5	4	0	3.00	3.00
Upland Sandpiper	Gx	3	2	3	5	3.14	3.00

Species found in the area but not confirmed nester on National Grassland.

CONCLUSIONS

The PIF species ranking system is a helpful tool in establishing priorities for Neotropical Migratory Bird species and habitat based management efforts for those species. It should not replace human judgment or additional information which might be important in setting resource priorities. Refinement of the PIF data as was done on the Oglala and Ft. Pierre National Grasslands with local expertise increases the utility value of the system. Only a few analysis examples were given here. However, an endless variety of queries can be used to tease additional information from the data.

ACKNOWLEDGMENTS

We acknowledge Greg Schenbeck, Wildlife Management Biologist for the Nebraska National Forest for providing information and suggestions to make this report possible.

LITERATURE CITED

Carter, Michael F. and Keith Barker., 1993. An Interactive Database for Setting Conservation Priorities for Western Neotropical Migrants. Pages 120-144 *in*. Finch and Stangel, eds. Status and Management of NTMB. USDA. Forest Service, General Technical Report RM 229.

Hunter, William C., David N. Pashley, and Ronald E.F. Escano. 1993. Neotropical Migratory Landbird Species and Their Habitats of Special Concern Within the Southeast Region. Pages 159-171 *in*. Finch and Stangel, eds. Status and Management of NTMB. USDA. Forest Service, General Technical Report. RM 229.

Master, L., 1991 Assessing threats and setting priorities for conservation. Cons. Biol. 5.559-563.

Millsap, B.A., J.A. Gore, D.E. Runde, and S.I. Cerulean. 1990. Setting priorities for the conservation of fish and wildlife species in Florida. Wildl. Monogr. 111.

Peterson, Richard A. 1994. Nebraska National Forest Neotropical Migrant Landbird Conservation Priorities. Unpubl. Rep. USDA Forest Service, Chadron. NE. 38pp.

Reed, Michael., 1992. A system for ranking conservation priorities for neotropical migrant birds based on relative susceptibility to extinction. Pp. 524-536. in Ecology and conservation of neotropical migrant landbirds. (J.M. Hagan III and D.W. Johnston, eds.). Washington and London, Smithsonian Institute.

Thompson, Frank R., Stephen J. Lewis, Janet Green and David Ewert. 1993. Status of NTM Landbirds in the Midwest: Identifying Species of Management concern. Pp. 145-153. in (Finch and Stangel (ed.). Status and Management of NTMB. USDA Forest Service, General Technical Report RM 229.

Appendix 1. Prioritization scores for the Neotropical Migratory Landbirds of the Oglala National Grasslands.

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
American Goldfinch	Tdes1	1.00	2.00	3.00	1.00	1.00	2.00	3.00	3.00	2.00	3.00	1.43	1.57
American Kestrel	Ec8	1.00	1.00	2.00	2.00	1.00	4.00	1.00	1.00	2.00	3.00	1.71	1.57
American Robin	Ethw	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00	4.00	3.00	1.57	1.29
Barn Swallow	Pgw5	1.00	1.00	1.00	2.00	1.00	2.00	1.00	1.00	5.00	1.00	1.86	1.29
Belted Kingfisher	W4	2.00	4.00	2.00	2.00	1.00	1.00	4.00	3.00	3.00	4.00	2.00	2.14
Black-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	3.00	2.00	3.00	3.00	4.00	3.00	3.29	3.14
Black-headed Grosbeak	Tdsl	2.00	3.00	4.00	2.00	3.00	2.00	2.00	3.00	2.00	2.00	2.57	2.57
Blue Grosbeak	Sn2	3.00	3.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.43	2.57
Bobolink	Ga39	2.00	4.00	2.00	3.00	3.00	1.00	5.00	2.00	5.00	2.00	3.14	3.14
Brewer's Blackbird	Es29	2.00	3.00	5.00	2.00	3.00	1.00	3.00	3.00	3.00	3.00	2.29	2.29
Brewer's Sparrow	Sb	2.00	4.00	3.00	4.00	3.00	1.00	5.00	1.00	4.00	3.00	3.00	3.14
Brown-headed Cowbird	Egsm	1.00	1.00	1.00	1.00	1.00	5.00	1.00	1.00	1.00	1.00	1.71	1.71
Burrowing Owl	Gh7	4.00	5.00	2.00	3.00	3.00	5.00	4.00	3.00	2.00	3.00	3.57	3.86
Cedar Waxwing	Ts	2.00	2.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.00	2.14
Chestnut-collared Longspur	Gxh	3.00	3.00	4.00	4.00	4.00	3.00	4.00	3.00	2.00	3.00	3.29	3.57
Chipping Sparrow	Efs	1.00	3.00	4.00	2.00	1.00	3.00	4.00	3.00	4.00	3.00	2.29	2.29
Cliff Swallow	Pw45	2.00	2.00	4.00	2.00	1.00	1.00	3.00	3.00	3.00	3.00	2.00	2.00
Common Nighthawk	Eh	2.00	2.00	4.00	2.00	1.00	5.00	3.00	3.00	4.00	3.00	2.43	2.29
Common Poorwill	Ef4	3.00	2.00	4.00	3.00	3.00	2.00	3.00	4.00	3.00	4.00	2.71	2.71
Common Yellowthroat	Wmsl	1.00	3.00	2.00	2.00	1.00	2.00	4.00	3.00	5.00	2.00	2.29	2.14
Cooper's Hawk	To1	3.00	3.00	3.00	3.00	1.00	1.00	3.00	4.00	3.00	5.00	2.29	2.29
Dickcissel	Ga9	2.00	4.00	3.00	2.00	3.00	1.00	5.00	1.00	4.00	3.00	2.86	3.00
Eastern Bluebird	Ec85	2.00	3.00	2.00	3.00	3.00	1.00	3.00	4.00	3.00	4.00	2.43	2.43
Eastern Kingbird	E	1.00	1.00	2.00	3.00	2.00	3.00	2.00	3.00	1.00	1.00	2.00	2.14
Eastern Phoebe	Td15	2.00	4.00	4.00	3.00	3.00	1.00	3.00	4.00	3.00	5.00	2.57	2.57
Ferruginous Hawk	Gxht7	4.00	4.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.29	3.29
Golden Eagle	Et47	3.00	2.00	2.00	2.00	2.00	5.00	4.00	3.00	2.00	3.00	2.57	2.86
Grasshopper Sparrow	Gxa	2.00	2.00	3.00	2.00	2.00	4.00	5.00	1.00	2.00	3.00	2.43	2.86
Gray Catbird	Sn12	2.00	4.00	2.00	2.00	2.00	2.00	4.00	2.00	2.00	3.00	2.43	2.71
Great Crested Flycatcher	Tdcl	2.00	4.00	3.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	3.00	3.00
Horned Lark	Gh7	1.00	1.00	1.00	1.00	1.00	5.00	2.00	2.00	2.00	3.00	1.71	1.71
House Wren	Tc15	1.00	2.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	2.00	1.29	1.29
Indigo Bunting	Tdsl	1.00	3.00	3.00	2.00	3.00	1.00	3.00	4.00	3.00	4.00	2.29	2.29
Killdeer	Gh67	1.00	2.00	2.00	1.00	1.00	5.00	4.00	1.00	5.00	1.00	2.29	2.14
Lark Bunting	Gxhs	2.00	3.00	3.00	3.00	4.00	5.00	4.00	2.00	3.00	3.00	3.29	3.43
Lark Sparrow	E	3.00	2.00	3.00	2.00	2.00	3.00	3.00	3.00	1.00	2.00	2.29	2.57
Lazuli Bunting	Tsl	2.00	3.00	4.00	2.00	3.00	2.00	4.00	3.00	2.00	3.00	2.57	2.86
Loggerhead Shrike	Es2	3.00	4.00	4.00	4.00	2.00	3.00	3.00	3.00	2.00	2.00	3.00	3.14
Long-billed Curlew	Gxh7	3.00	3.00	4.00	3.00	4.00	5.00	4.00	3.00	5.00	1.00	3.86	3.71
Long-eared Owl	Efo0	3.00	3.00	3.00	3.00	1.00	1.00	3.00	5.00	3.00	5.00	2.14	2.14

Appendix 1 (Continued).

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
Marsh Wren	Wm	2.00	4.00	2.00	4.00	3.00	2.00	3.00	4.00	3.00	4.00	2.71	2.71
Merlin	Ef0	4.00	4.00	4.00	3.00	2.00	2.00	3.00	4.00	3.00	4.00	2.86	2.86
Mountain Bluebird	Ec85	2.00	3.00	3.00	3.00	3.00	2.00	4.00	2.00	3.00	3.00	2.57	2.71
Mourning Dove	Ew	1.00	1.00	1.00	1.00	1.00	4.00	1.00	1.00	3.00	3.00	1.71	1.43
N. Rough-winged Swallow	Pw4	3.00	3.00	3.00	2.00	1.00	2.00	4.00	3.00	3.00	3.00	2.43	2.57
Northern Flicker	Ec8	1.00	2.00	1.00	1.00	1.00	2.00	4.00	2.00	3.00	3.00	1.57	1.71
Northern Harrier	Gasm	3.00	4.00	3.00	4.00	1.00	3.00	4.00	3.00	4.00	3.00	2.86	2.86
Northern Mockingbird	Eds12	1.00	2.00	2.00	1.00	2.00	1.00	3.00	4.00	3.00	4.00	1.71	1.71
Northern Oriole	Tdsl	2.00	3.00	3.00	2.00	2.00	2.00	3.00	3.00	3.00	3.00	2.43	2.43
Orchard Oriole	Tdsl	3.00	3.00	3.00	2.00	3.00	2.00	2.00	2.00	4.00	3.00	2.86	2.57
Oven bird	Tu	2.00	4.00	4.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	2.86	2.86
Pine Siskin	Tfe	1.00	2.00	3.00	1.00	2.00	2.00	3.00	4.00	3.00	4.00	1.71	1.71
Prairie Falcon	Gxh47	3.00	3.00	3.00	3.00	3.00	4.00	3.00	3.00	4.00	3.00	3.14	3.00
Red-eyed Vireo	Tdul	1.00	4.00	4.00	2.00	2.00	1.00	3.00	3.00	3.00	4.00	2.29	2.29
Red-tailed Hawk	Etg	1.00	2.00	2.00	2.00	1.00	5.00	3.00	3.00	3.00	3.00	2.14	2.14
Red-winged Blackbird	Wms1	1.00	2.00	1.00	1.00	1.00	2.00	4.00	2.00	4.00	3.00	1.71	1.71
Rock Wren	P4	3.00	2.00	2.00	2.00	3.00	3.00	4.00	2.00	4.00	3.00	2.71	2.71
Rufous-sided Towhee	Sn	1.00	3.00	4.00	2.00	2.00	2.00	4.00	3.00	4.00	3.00	2.29	2.29
Say’s Phoebe	G45	3.00	2.00	3.00	3.00	2.00	3.00	3.00	3.00	3.00	3.00	2.71	2.71
Sharp-shinned Hawk	Tfo	3.00	3.00	2.00	3.00	1.00	1.00	3.00	4.00	3.00	4.00	2.14	2.14
Short-eared Owl	Gasm	3.00	4.00	4.00	4.00	1.00	2.00	2.00	3.00	4.00	3.00	2.71	2.43
Swainson’s Hawk	Gxt9	3.00	2.00	2.00	3.00	2.00	5.00	2.00	1.00	2.00	3.00	2.86	2.86
Tree Swallow	Ec15	2.00	4.00	3.00	3.00	1.00	1.00	2.00	3.00	3.00	3.00	2.29	2.14
Turkey Vulture	E4	1.00	2.00	4.00	2.00	1.00	4.00	2.00	2.00	4.00	3.00	2.14	1.86
Upland Sandpiper	Gx	3.00	2.00	3.00	3.00	3.00	4.00	2.00	3.00	3.00	3.00	3.00	2.86
Vesper Sparrow	Gxs	3.00	3.00	4.00	2.00	2.00	2.00	4.00	3.00	4.00	3.00	2.57	2.57
Violet-green Swallow	Efc4	2.00	3.00	3.00	2.00	3.00	2.00	3.00	4.00	3.00	4.00	2.57	2.57
Warbling Vireo	Td1	2.00	3.00	4.00	2.00	2.00	2.00	5.00	1.00	4.00	3.00	2.57	2.71
Western Kingbird	E	1.00	1.00	2.00	2.00	3.00	3.00	1.00	1.00	1.00	2.00	2.14	2.14
Western Meadowlark	Gx7	1.00	2.00	2.00	3.00	2.00	5.00	3.00	3.00	3.00	3.00	2.43	2.43
Western Tanager	Tf	2.00	3.00	4.00	2.00	3.00	2.00	3.00	4.00	3.00	4.00	2.57	2.57
Western Wood-Pewee	T	2.00	3.00	4.00	3.00	2.00	2.00	2.00	2.00	1.00	1.00	2.43	2.57
White-throated Swift	P4	3.00	2.00	3.00	2.00	3.00	1.00	3.00	4.00	3.00	4.00	2.43	2.43
Willow Flycatcher	**Sn12**	3.00	4.00	3.00	3.00	3.00	1.00	3.00	5.00	4.00	3.00	3.00	2.86
Yellow Warbler	Tds1	1.00	4.00	3.00	2.00	1.00	2.00	2.00	3.00	2.00	3.00	1.86	1.86
Yellow-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	2.00	2.00	2.00	3.00	3.00	4.00	2.86	2.71
Yellow-breasted Chat	Sn12	2.00	3.00	3.00	3.00	2.00	2.00	3.00	3.00	1.00	1.00	2.29	2.57
Yellow-headed Blackbird	Wm	3.00	4.00	2.00	3.00	3.00	2.00	2.00	3.00	4.00	3.00	3.14	2.86
Yellow-rumped Warbler	Tf	1.00	2.00	2.00	1.00	1.00	2.00		4.00	3.00	4.00	1.71	1.29

Appendix 2. Prioritization scores for the Neotropical Migratory Landbirds of the Ft. Pierre National Grasslands.

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
American Goldfinch	Tdes1	1.00	2.00	3.00	1.00	1.00	2.00	3.00	3.00	2.00	3.00	1.43	1.57
American Kestrel	Ec8	1.00	2.00	2.00	2.00	1.00	4.00	1.00	1.00	2.00	3.00	1.86	1.71
American Robin	Ethw	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00	4.00	3.00	1.57	1.29
Baird's Sparrow(historic)	Gx3	4.00	5.00	4.00	4.00	5.00	0.00	4.00	3.00	5.00	2.00	3.86	3.71
Bank Swallow	Pw4	3.00	3.00	4.00	2.00	1.00	1.00	2.00	3.00	2.00	2.00	2.14	2.14
Barn Swallow	Pgw5	1.00	1.00	1.00	2.00	1.00	2.00	1.00	1.00	5.00	1.00	1.86	1.29
Bell's Vireo	Sn12	3.00	4.00	3.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	3.14	3.14
Belted Kingfisher	w4	2.00	4.00	2.00	2.00	1.00	1.00	4.00	3.00	3.00	4.00	2.00	2.14
Black-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	3.00	2.00	3.00	3.00	4.00	3.00	3.29	3.14
Black-headed Grosbeak	Tds1	2.00	3.00	4.00	2.00	3.00	1.00	2.00	3.00	2.00	2.00	2.43	2.43
Blue Grosbeak	Sn2	3.00	3.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.43	2.57
Bobolink	Ga39	2.00	3.00	2.00	3.00	3.00	3.00	5.00	2.00	5.00	2.00	3.29	3.29
Brown-headed Cowbird	Egsm	1.00	1.00	1.00	1.00	1.00	5.00	1.00	1.00	1.00	1.00	1.71	1.71
Burrowing Owl	Gh7	4.00	5.00	2.00	3.00	3.00	5.00	4.00	3.00	2.00	3.00	3.57	3.86
Cedar Waxwing	Ts	2.00	3.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.14	2.29
Chestnut-collared Longspur	Gxh	3.00	3.00	4.00	4.00	4.00	3.00	4.00	3.00	2.00	3.00	3.29	3.57
Chipping Sparrow	Efs	1.00	3.00	4.00	2.00	1.00	1.00	4.00	3.00	4.00	3.00	2.00	2.00
Cliff Swallow	Pw45	2.00	2.00	4.00	2.00	1.00	1.00	3.00	3.00	3.00	3.00	2.00	2.00
Common Nighthawk	Eh	2.00	2.00	4.00	2.00	1.00	5.00	3.00	3.00	4.00	3.00	2.43	2.29
Common Yellowthroat	Wms1	1.00	3.00	2.00	2.00	1.00	2.00	4.00	3.00	5.00	2.00	2.29	2.14
Dickcissel	Ga9	2.00	3.00	3.00	2.00	3.00	5.00	5.00	1.00	4.00	3.00	3.29	3.43
Eastern Bluebird	Ec85	2.00	3.00	2.00	3.00	3.00	1.00	3.00	4.00	3.00	4.00	2.43	2.43
Eastern Kingbird	E	1.00	1.00	2.00	3.00	2.00	3.00	2.00	3.00	1.00	1.00	2.00	2.14
Eastern Phoebe	Td15	2.00	4.00	4.00	3.00	3.00	1.00	3.00	4.00	3.00	5.00	2.57	2.57
Ferruginous Hawk	Gxht7	4.00	4.00	3.00	3.00	3.00	4.00	3.00	3.00	3.00	3.00	3.43	3.43
Grasshopper Sparrow	Gxa	2.00	2.00	3.00	2.00	2.00	5.00	5.00	1.00	2.00	3.00	2.57	3.00
Gray Catbird	Sn12	2.00	4.00	2.00	2.00	2.00	1.00	4.00	2.00	2.00	3.00	2.29	2.57
Great Crested Flycatcher	Tdc1	2.00	4.00	3.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	3.00	3.00
Horned Lark	Gh7	1.00	1.00	1.00	1.00	1.00	5.00	2.00	2.00	2.00	3.00	1.71	1.71
House Wren	Tc1	1.00	2.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	2.00	1.29	1.29
Indigo Bunting	Tds1	1.00	3.00	3.00	2.00	3.00	1.00	3.00	4.00	3.00	4.00	2.29	2.29
Killdeer	Gh67	1.00	2.00	2.00	1.00	1.00	5.00	4.00	1.00	5.00	1.00	2.29	2.14
Lark Bunting	Gxhs	2.00	3.00	3.00	3.00	4.00	5.00	4.00	2.00	3.00	3.00	3.29	3.43
Lark Sparrow	E	3.00	2.00	3.00	2.00	2.00	2.00	3.00	3.00	1.00	2.00	2.14	2.43
Least Flycatcher	Td1	3.00	4.00	5.00	4.00	2.00	1.00	3.00	3.00	2.00	3.00	2.71	2.86

Appendix 2 (Continued).

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
Loggerhead Shrike	Es2	3.00	4.00	4.00	4.00	2.00	2.00	3.00	3.00	2.00	2.00	2.86	3.00
Long-billed Curlew	Gxh7	3.00	4.00	4.00	3.00	4.00	1.00	4.00	3.00	5.00	1.00	3.43	3.29
Long-eared Owl	Efo0	3.00	3.00	3.00	3.00	1.00	1.00	3.00	5.00	3.00	5.00	2.14	2.14
Marsh Wren	Wm	2.00	4.00	2.00	4.00	3.00	1.00	3.00	3.00	3.00	4.00	2.57	2.57
Mourning Dove	Ew	1.00	1.00	1.00	1.00	1.00	4.00	1.00	1.00	3.00	3.00	1.71	1.43
N. Rough-winged Swallow	Pw4	3.00	3.00	3.00	2.00	1.00	2.00	4.00	3.00	3.00	3.00	2.43	2.57
Northern Flicker	Ec8	1.00	2.00	1.00	1.00	1.00	2.00	4.00	2.00	3.00	3.00	1.57	1.71
Northern Harrier	Gasm	3.00	3.00	3.00	4.00	1.00	5.00	4.00	3.00	4.00	3.00	3.00	3.00
Northern Mockingbird	Eds12	1.00	2.00	2.00	1.00	2.00	1.00	3.00	4.00	3.00	4.00	1.71	1.71
Northern Oriole	Tdsl	2.00	3.00	3.00	2.00	2.00	2.00	3.00	3.00	3.00	3.00	2.43	2.43
Orchard Oriole	Tdsl	3.00	3.00	3.00	2.00	3.00	3.00	2.00	2.00	4.00	3.00	3.00	2.71
Red-eyed Vireo	Tdul	1.00	4.00	4.00	2.00	2.00	1.00	3.00	3.00	3.00	4.00	2.29	2.29
Red-tailed Hawk	Etg	1.00	2.00	2.00	2.00	1.00	5.00	3.00	3.00	3.00	3.00	2.14	2.14
Red-winged Blackbird	Wms1	1.00	2.00	1.00	1.00	1.00	3.00	4.00	2.00	4.00	3.00	1.86	1.86
Rock Wren	P4	3.00	3.00	2.00	2.00	3.00	1.00	4.00	2.00	4.00	3.00	2.57	2.57
Rufous-sided Towhee	Sn	1.00	3.00	4.00	2.00	2.00	2.00	4.00	3.00	4.00	3.00	2.29	2.29
Savannah Sparrow	Gx3	3.00	4.00	4.00	3.00	1.00	1.00	5.00	1.00	5.00	1.00	2.71	2.71
Say’s Phoebe	G45	3.00	2.00	3.00	3.00	2.00	1.00	3.00	3.00	3.00	3.00	2.43	2.43
Short-eared Owl	Gasm	3.00	3.00	4.00	4.00	1.00	5.00	2.00	3.00	4.00	3.00	3.00	2.71
Sprague’s Pipit (historic)	Gxa	3.00	5.00	5.00	3.00	4.00	0.00	3.00	3.00	3.00	3.00	3.00	3.00
Swainson’s Hawk	Gxt9	3.00	2.00	2.00	3.00	2.00	5.00	2.00	1.00	2.00	3.00	2.86	2.86
Tree Swallow	Ec15	2.00	3.00	3.00	3.00	1.00	1.00	2.00	3.00	3.00	3.00	2.14	2.00
Turkey Vulture (no nest?)	E4	1.00	2.00	4.00	2.00	1.00	1.00	2.00	2.00	4.00	3.00	1.71	1.43
Upland Sandpiper	Gx	3.00	2.00	3.00	3.00	3.00	5.00	2.00	3.00	3.00	3.00	3.74	3.00
Vesper Sparrow	Gxs	3.00	3.00	4.00	2.00	2.00	1.00	4.00	3.00	4.00	3.00	2.43	2.43
Warbling Vireo	Td1	2.00	4.00	4.00	2.00	2.00	2.00	5.00	1.00	4.00	3.00	2.71	2.86
Western Kingbird	E	1.00	1.00	2.00	2.00	3.00	3.00	1.00	1.00	1.00	2.00	2.14	2.14
Western Meadowlark	Gx7	1.00	2.00	2.00	3.00	2.00	5.00	3.00	3.00	3.00	3.00	2.43	2.43
Willow Flycatcher	Sn12	3.00	4.00	3.00	3.00	3.00	1.00	3.00	5.00	4.00	3.00	3.00	2.86
Yellow Warbler	Tdsl	1.00	4.00	3.00	2.00	1.00	2.00	2.00	3.00	2.00	3.00	1.86	1.86
Yellow-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	2.00	1.00	2.00	3.00	3.00	4.00	2.71	2.43
Yellow-breasted Chat	Sn12	2.00	3.00	3.00	3.00	2.00	1.00	3.00	3.00	1.00	1.00	2.14	2.43
Yellow-headed Blackbird	Wm	3.00	3.00	2.00	3.00	3.00	2.00	2.00	3.00	4.00	3.00	3.00	2.71

Greater Prairie Chicken Nesting Habitat, Sheyenne National Grassland, North Dakota

Clinton McCarthy[1], Tim Pella[2], Greg Link[3], and Mark A. Rumble[4]

Abstract.-Greater prairie chicken *(Tympanuchus cupido pinnatus)* populations and habitats have declined dramatically in the Great Plains. The Sheyenne National Grassland (SNG) has the largest population of greater prairie chickens in North Dakota, but this population has declined over the past 15 years. Lack of nesting habitat has been identified as a significant factor contributing to the decline in greater prairie chicken populations throughout their range. We used the Habitat Suitability Index (HSI) model for greater prairie chickens to evaluate the nesting habitat conditions on the SNG. This population of greater prairie chickens appears to sustain itself on the brink of extirpation by nesting in the few areas that provide nesting cover and in private alfalfa fields. Encroachment of woody plants into the SNG, changes in private land-use patterns, removal of forage by domestic livestock contribute to the low suitability of the SNG for nesting by greater prairie chickens.

INTRODUCTION

The Sheyenne National Grassland (SNG) is approximately 28,745 ha of federally administered prairie in southeastern North Dakota. Within its administrative boundary there are an additional 25,910 ha of interspersed private cropland and prairie. The SNG contains the largest population of greater prairie chickens *(Tympanuchus cupido pinnatus)* in the state of North Dakota (Kobriger et al. 1987). Greater prairie chickens are not native to the SNG, but are considered a naturalized immigrant in North Dakota (Johnson and Knue 1989). Prairie chickens apparently moved into North Dakota from the north-central part of the United States during the Euro-American settlement in the 1870's and 1880's (Johnson and Knue 1989, Evans 1968). Greater prairie chicken populations and their habitats (native tall grass prairie) have declined to a small fraction of their historical range (Hjertaas et al. 1993, Samson and Knopf 1994). Thus, the population of greater prairie chickens on the SNG has both regional and national importance.

Numbers of prairie chickens on the SNG increased from the early 1960's through the early 1980's (Kobriger et al. 1987). Since then, prairie chicken numbers on the SNG have declined from a high of 410 males in 1983 to a low of 84 males in 1994 (Kobriger et al. 1987, unpubl. data, Sheyenne National Grassland, Lisbon, ND). State and federal natural resource management agencies, and conservation groups are concerned that management of the SNG may be contributing to the decline in the greater prairie chicken population. Lack of suitable nesting habitat has been identified as the most significant factor limiting populations of greater prairie chickens across their range (Kirsch 1974, Westemeir 1973) and in North Dakota (Svedarsky 1979).

Habitat suitability index (HSI) models are an accepted method for quantifying species' habitats as numerical index (Schamberger et al. 1982). Biological and habitat information are synthesized to formulate index values between zero (unsuitable) and one (optimum) for habitat requisites considered important to a species (U.S. Fish and Wildlife Service 1980). We conducted HSI analyses to assess habitat conditions for greater prairie chickens on the SNG at three scales: 1) the western portion of the SNG and adjacent private lands, 2) the Durler/Venlo Management unit, and 3) areas $\leq$1.6 km of the 14 active booming grounds.

METHODS

The HSI model for greater prairie chickens (Prose 1985) identifies two habitat components, nesting cover and winter food, as the most important habitat

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ponents for prairie chickens. The HSI for nesting cover is based on grassland vegetation height/density (expressed as visual obstruction measurements on a pole, Robel et al. 1970) for nesting cover in the spring (figure 1).

We mapped the lowland, midland, and upland grassland vegetation types (Manske and Barker 1987) on 1:24,000 aerial photos of the SNG. Most nesting by greater prairie chickens on the SNG occurs within 1.6 km of leks (Newell et al. 1987). The Custer National Forest Land Management Plan (U.S. Forest Service, Custer National Forest, Billings, MT, 1986) requires that nesting habitat for prairie grouse be assessed within 1.6 km of leks. During October and November, 1994, we estimated height/density of vegetation in these vegetation types from 81 transects within 1.6 km of greater prairie chicken leks in the northern and western portion of the SNG. At each of 10 stations on each transect, we recorded the height that vegetation obstructed 100 percent of a pole (VOR) marked in 0.5 dm increments when viewed from four directions (at 90” azimuths) at a distance of 4 m and a height of 1 m from the pole (Robel et al. 1970). VORs were averaged for each station and the average among stations was used to estimate transect VORs. We placed six transects in upland vegetation, 51 transects in midland vegetation and 26 transects in lowland vegetation. Data from these transects were used as VOR estimates in the mapped vegetation polygons they were collected in. For all other mapped vegetation polygons, these VOR data served as calibrations for ocular estimates of five VOR classes (0 - 0.50 dm, 0.51 - 1.0 dm, 1.01 - 1.5 dm, 1.51 - 2.0 dm, and >2.0 dm) during field reconnaissance. Maps of vegetation and VOR class assignments were transferred to 1:24,000 U.S. Geological Survey maps and the area of each vegetation was planimetered for use in the HSI estimates.

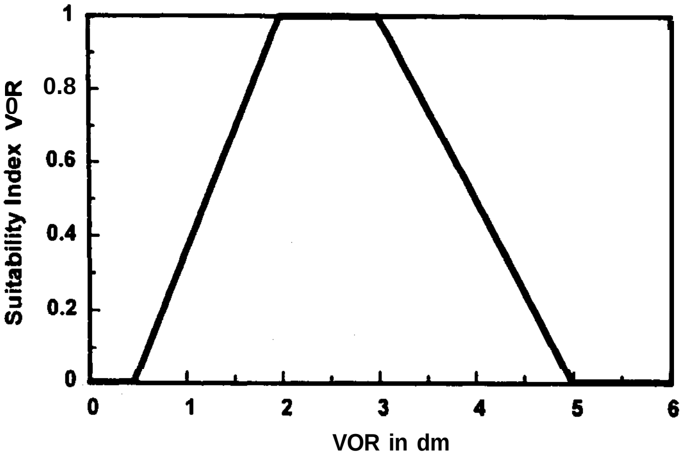

Figure 1. Relationship between average 100 percent obstruction of pole (VOR) marked in 0.5 dm increments and next cover suitability index for greater prairie chickens (from Prose 1985).

HSI for nesting cover is estimated in three steps (Prose 1985). First, a suitability index is estimated from the midpoint of the VOR classes of each vegetation type i (SI_{VORi}). Second, the percent of area providing equivalent optimal nesting habitat (EONH) is calculated using:

$$EONH = \sum_{i=1}^{n} (SI_{VOR_i})(N_i)$$

where n = total number of vegetation types, and N = percent of the area in vegetation type i. Third, HSI for nest cover is calculated from:

$$HSI = \frac{(0.735 * EONH) - 21.4}{37}$$

Characteristics of vegetation and winter snow accumulation influence the structure of vegetation in the spring for nesting by greater prairie chickens. VOR measurement collected in the fall decrease prior to spring nesting. This decrease is proportional to the height of vegetation and for the range of VOR 0.5 - 2.0 dm varies from 7-40 percent in mixed grass prairie (G. Schenbeck pers. commun., Nebraska National Forest, Chadron, NE). Over winter VOR losses on the SNG are probably different, but data are lacking. We selected 15 percent over-winter VOR losses to estimate spring nesting cover based on fall VOR estimates because the VORs for the SNG are near the lower end of the range.

Western SNG Analysis

The western part of the SNG includes most of the prairie chicken leks. This area included 3433 ha of private land and 8984 ha of SNG administered lands. We calculated the HSI for this analysis unit to show estimated contributions to the HSI for prairie chickens from adjacent private lands. VOR class tion was available for only 5738 ha (64 percent) of the SNG lands in this analysis unit. We assumed the mapped VOR classes were representative of the remaining of the western SNG and used these data for HSI calculations in this analysis unit. For private lands in the western SNG analysis unit we assumed: 1) CRP land had VOR class > 2.0 dm; 2) hay and alfalfa had VOR cover classes <0.5 dm because of mowing approximately the third week of June that destroys existing nests and most young hatched birds; and 3) grazed pasture had VOR cover class 0.51-1.0 dm.

Durler/Venlo Management Unit

The Durler/Venlo management unit includes 3645 ha in nine range management allotments in the western SNG. The Durler/Venlo unit is a subset of the prairie chicken range in the western portion of the SNG. It includes the larger leks, highest prairie chicken numbers, and the greatest number of prairie chicken leks not shared by sharp-tailed grouse (*Tympanuchus phasianellus jamesi).* Most of the Durler/Venlo management unit is< 1.6 km from a prairie chicken lek. This portion of SNG has complete vegetation classification and mapping.

We excluded vegetation communities that were not available for nesting by greater prairie chickens from the HSI for the Durler/Venlo management unit. This HSI analysis presents a complete picture of the nesting habitat for this area. We assigned vegetation types to mapped polygons using the dominant vegetation community in the polygons. Within these polygons, vegetation communities not capable of producing 1.5 dm VOR measurements or that are usually flooded (Manske and Barker 1987, Newell et al. 1987) were considered unavailable for nesting by greater prairie chickens. The area in each polygon assigned to a VOR class did not include unsuitable areas. For example, lowland vegetation communities dominated by species such as *Carex lanulosa* were considered unavailable because in most years the ground is flooded. Upland vegetation communities dominated by species such as *Boutelou gracilis* were considered unavailable for prairie chicken nesting because they are not capable of producing at least 1.5 dm VOR in most years.

Area Surrounding 14 Active Leks

The area within 1.6 km of active leks includes most of the nesting habitat of greater prairie chickens. This scale of analysis allowed us to evaluate HSI for areas of known greater prairie chicken occurrences. This level of analysis included the area surrounding active greater prairie chicken leks and we expected HSI from this analysis should equal or exceed the HSI's from the blocks of SNG that included areas > 1.6 km from leks and unused areas.

RESULTS

Western Sheyenne National Grassland

The 12,445 ha in the western SNG had 24 percent EONH (table 1), less than the minimum considered necessary for the HSI to be greater than zero using fall VOR estimates. When over-winter VOR losses were included, the EONH in the spring declined to 21 percent, with an HSI remaining zero.

Durler/Venlo Management Unit

EONH in the Durler/Venlo unit was lower that the western SNG. EONH was reduced by eliminating the lowlands that are usually flooded in the spring from the HSI calculations. The net result was 12 percent fall EONH and 9 percent EONH in the spring. The subsequent HSI for the Durler/Venlo unit was also zero.

Table 1. Percent equivalent optimal nesting habitat and nesting HSI for three analysis areas with and without winter VOR loss on the Sheyenne National Grassland.

Analysis area	Percent EONH[1]	HSI	Percent EONH with overwinter VOR loss	HSI
Western SNG	23.8	0	19.8	0
Durler/Venlo	11.7	0	9.3	0
≤1 .6 km leks	25.7	0	21.1	0

[1] EONH = equivalent optimum nesting habitat as defined in HSI model by Prose 1985).

Area Surrounding 14 Active Leks

The area within 1.6 km of the 14 active leks had a larger EONH (26 percent) in the fall than the other analysis units. However, the nesting HSI was zero for this area as well. Four of the lek areas provided sufficient EONH for HSI's greater than zero. However HSI estimates for spring showed that only two of these leks still provided sufficient EONH for HSI's greater than zero.

DISCUSSION

Nesting HSI

Our data suggests that nesting cover limits greater prairie chicken populations on the SNG. HSI's were zero for all the analysis units we compared. Four leks had sufficient nesting cover in the surrounding 1.6 km for HSI's greater than zero based on the fall measurements. HSI for these lek areas were less than 0.2 Only two leks had HSI's greater than zero for the area within 1.6 km from leks after over winter VOR losses were considered. HSI's for these two leks were ≤ 0.1

VOR measurements in grassland vegetation that are 2 to 3 dm are considered optimal nest cover for greater prairie chickens (Prose 1985). VOR measurements > 1.5 dm provide $SI_{VOR} > 0.7$. Only 16 percent of the western SNG was in the VOR class > 1.5 dm. In the Durler/Venlo management unit, only 7 percent of the suitable nesting area provided vegetation > 1.5 dm. For areas (1.6 km of leks, only 14 percent of the area had vegetation in the >1.5 dm VOR classes. Suitable nesting cover for prairie chickens may increase during drought years because lowlands that are usually flooded are drier and usable for nesting by hens.

Most of the nesting habitat for greater prairie chickens in the SNG is the midland community type in the humocky sandhills (Manske and Barker 1981, Manske and Barker 1987). Switchgrass *(Panicum virgatum)* communities found on the toe slopes surrounding lowland meadows provide the primary prairie chicken nesting cover on the SNG (Manske and Barker 1987, Newell 1987). Although lowlands are not considered suitable for nesting in most years, the lowland/midland interface is used for nesting by prairie chickens (Newell 1987). The lack of adequate cover for nesting in upland communities was attributed to heavy livestock utilization (Newell 1987). Historically, upland communities were likely tall grass prairie (Burgess 1964), but currently have limited capacity to provide nesting cover because they are dominated by short cool season and warm season grasses such as Kentucky bluegrass and blue grama.

The HSI model (Prose 1985) assumes that optimum nesting habitat conditions exist when 80 percent of the area supports herbaceous vegetation with a VOR of 2 - 3 dm. However, lingering populations of greater prairie chickens can exist in areas with 10-15 percent permanent grassland (Hamerstrom et al. 1957, Prose 1985). Topfer et al. (1990) considers a spring population of 200 birds (100 males) as a minimum number to insure perpetuation of the population. Greater prairie chickens probably persist on the SNG because natural variation provides small limited areas with adequate nesting cover. These areas exist at the lowland/midland community interface, in lowlands during drought years, and in limited quantity surrounding some leks. Limited nesting also occurs in alfalfa on private lands (Newell 1987). Small populations, such as the greater prairie chicken on the SNG, are highly susceptible to extinction due to catastrophic natural events (Ruggiero et al. 1994).

Robustness of Analyses to Assumptions

Because the HSI in our evaluation were based on ocular estimates of VOR classes, we conducted analyses to estimate HSI for systematic errors in estimating the VOR classes. If we over estimated the VOR classes (e.g.,VOR was actually lower), then HSI would decline further. Because, the lower limit on HSI is zero, our conclusion of limited nesting habitat remained unchanged.

If we systematically underestimated VOR classes by one class (0.5 dm), HSI for the Western SNG increased to 0.1 for fall VOR estimates and remained zero for estimates of spring nesting cover. HSI in the Durler/Venlo unit remained zero for both spring and fall VOR estimates. HSI for the areas around active leks increased to 0.3 for fall VOR estimates, but declined to 0.1 for spring estimates of nesting cover. Because the area surrounding leks included lowlands that are flooded in most years, the HSI was probably lower. None-the-less, analyses that assume we underestimated nesting cover, still show that nesting habitat is limited on the SNG.

The VOR estimates we used for the 3433 ha private lands in western SNG analysis unit were made subjectively post hoc. Because, these post hoc estimates of private land VOR may have influenced the HSI, we conducted an analysis that would present the best possible HSI for this analysis unit. HSI for the western SNG was recalculated assigning all private lands with suitable vegetation types (hay and alfalfa, pastures, and CRP) for nesting, a SI_{VOR} of 1.0 (this analysis does not change the HSI for nest cover on lands managed by the SNG). The resulting HSI for nest cover increased for the western SNG analysis unit to 0.33. This HSI represents the upper limit for the western SNG analysis unit, but it is not realistic. Most of the area considered to have SI_{VOR} of 1.0 are grazed or mowed annually. Hay and alfalfa is usually cut by the third week of June, destroying existing nests and young broods unable to escape the mowers. Only the 251 ha of CRP in the analysis unit maintained its structural integrity throughout the nesting and brood rearing periods. None-the-less, this analysis still indicated that regional nesting habitat for greater prairie chickens is limited in the vicinity of the SNG.

Contributing Factors

The encroachment of woody and exotic plant species, changes in adjacent agricultural/land use changes, and livestock grazing practices are three human induced factors that directly or and indirectly influence nesting cover for prairie chickens on the SNG. Quaking aspen *(Populus tremuloides)*, willow *(Salix* spp.) and Russian olive *(Elaeagnus angustifolia)* have encroached into prairie reducing nesting cover on the SNG (Kobriger et al. 1987, Jensen 1992). Leafy spurge *(Euphorbia esula)* has expanded from 7 percent to over 17 percent of the SNG since 1985 (unpubl. data, SNG). Encroachment of woody plants reduces and fragments suitable nesting, brood rearing and roosting cover (Svedarsky 1979); provides travel corridors and perch sites for predators (Burhnerkempe et al. (1984) and creates habitat more suitable for closely related sharp-tailed grouse (Prose 1987).

Agricultural development on private lands adjacent to the SNG over the past 10-15 years shows that remnant prairie habitats on private lands have been largely converted to croplands (unpubl. data, Nat. Res. Conserv. Serv., Lisbon, ND). Our analysis of the western SNG unit, showed that most of the suitable nesting habitat on private lands was Conservation Reserve Program comprising 250 ha in the analysis unit. No privately owed parcels of native prairie were identified in our analysis of the western SNG.

Grazing by livestock is the predominant use of the SNG. Livestock stocking rates have fluctuated between 50,000 and 60,000 AUMs over the past 10 - 15 years on the SNG. However, the size of livestock has increased approximately 40 percent during a comparable period (L. Potts, pers. commun., SNG, Lisbon, ND). These heavier animals require approximately 30 percent more forage (National Research Council 1984) than the standard AUM established for a 454 kg animal.

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LITERATURE CITED

Burgess, R. L. 1964. Ninety years of vegetational change in a township in southeastern North Dakota. Proc. North Dakota Acad. Sci. 18:84-94.

Burhnerkempe, J. E.; Edwards, W. R.; Vance, D. R.; Westemeir, R. L. 1984. Effects of residual vegetation on prairie chicken nest placement and success. Wildl. Soc. Bull. 12:382-386.

Evans, K. E. 1968. Characteristics and habitat requirements of the greater prairie chicken and sharp-tailed grouse: a review of the literature. Cons. Res. Rep. No. 12. Fort Collins, CO: U. S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 32 p.

Hamerstrom, F. N. Jr; Mattsen, 0. E.; Hamerstrom, F. 1957. A guide to prairie chicken management. Tech. Bull. 15. Madison, WI: Wisconsin Conservation Department. 128 p.

Hjertaas, H; et al. 1993. National recovery plan for the greater prairie chicken. Renewable Rep. No. 5, Ottawa, Ontario: Canadian Wildlife Federation. 18 p.

Jensen, W. F. 1992. Historical review of prairie chicken management on the Sheyenne National Grassland. Unpublished Report. Bismarck, ND: North Dakota Game and Fish Department.

Johnson, M. D.; Knue, J. 1989. Pinneated grouse. In: Feathers from the prairie. Bismarck, ND: North Dakota Game and Fish Department: 97-122.

Kirsch, L. M. 1974. Habitat management considerations for prairie chickens. Wildl. Soc. Bull. 2:124-129.

Kobriger, G. D.; Vollind, D. I?; McNeill, M. E.; Higgins, K. F. 1987. Prairie chicken populations of the Sheyenne Delta North Dakota 1961-1987. pp. 1-7. In: A. J. Bjugstad, tech. coord. Prairie Chickens on the Sheyenne National Grasslands. Gen. Tech. Rep. RM-159. Fort Collins, CO: U. S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station. 73 p.

Manske, L. L.; Barker, W. T. 1981. The prairie grouse on the Sheyenne National Grasslands. Unpublished Report. Fargo, ND: North Dakota State Univ. 238 p.

Manske, L. L.; Barker, W. T. 1987. Habitat Usage by prairie grouse on the Sheyenne National Grasslands. pp. 8-20. In: A. J. Bjugstad, tech. coord. Prairie Chickens on the Sheyenne National Grasslands. Gen. Tech. Rep. RM-159. Fort Collins, CO: U. S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station. 73 p.

National Research Council. 1984. Nutrition requirements for beef cattle, sixth revised edition. Washington, D. C.: National Academy Press. 90 p.

Newell, J. A. 1987. Nesting and brood rearing ecology of the greater prairie chicken in the Sheyenne National Grasslands, North Dakota. Boseman, MT: Montana State University. 111 p. M. S. thesis.

Newell, J. A.; Toepfer. J. E.; Rumble; M. A. 1987. Summer brood rearing ecology of the greater prairie chicken on the Sheyenne National Grasslands. pp. 24-31. In: A. J. Bjugstad, tech. coord. Prairie Chickens on the Sheyenne National Grasslands. Gen. Tech. Rep. RM-159. Fort Collins, CO: U. S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station. 73 p.

Prose, B. L. 1985. Habitat suitability index models: greater prairie chicken (multiple levels of resolution). Biol. Rep. 82 (10.102). Fort Collins, CO: U. S. Department of Interior, Fish and Wildlife Service. 33 p.

Prose, B. L. 1987. Habitat suitability index models: plains sharp-tailed grouse. Biol. Rep. 82(10.142). Fort Collins, CO: U. S. Department of Interior, Fish and Wildlife Service. 31 p.

Robel, L. J.; Briggs, J. N; Dayton, A. D.; Hulbert, L. C. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. J. Range Manage. 23:295-297.

Ruggiero, L. F.; Hayward, G. D.; Squires, J. R. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population and ecological scale. Conserv. Biol. 8:364-372.

Toepfer, J. E.; Eng, R. L.; Anderson, R. K. 1990. Translocation of prairie grouse: what have we learned? Trans. N. Amer. Nat. Resour. Conf. 55:569-579.

Samson, F.; Knopf, F. 1994. Prairie conservation in North America. Bioscience 44:418-421.

Shamberger, M. A.; Farmer, A. H.; Terrell, J. W. 1982. Habitat suitability index models: introduction. FWSI OBS-82/10. Fort Collins, CO: U. S. Department of Interior, Fish and Wildlife Service. Western Energy and Land Use Team. 2 p.

Svedarsky, W. D. 1979. Spring and summer ecology of female greater prairie chickens in northwestern Minnesota. Grand Forks, ND: University of North Dakota. 166 p. Ph. D. dissertation.

Westemeir, R. L. 1973. Prescribed burning in grassland management for prairie chickens in Illinois. In: Proceeding, 12th annual Tall Timbers Fire Ecology Conference. June 8-9, 1972. Lubbock, TX. Tallahassee, FL: Tall Timbers Research Station; 12:317-338.

U. S. Fish and Wildlife Service. 1980. Habitat as the basis for environmental assessment. Ecol. Serv. Man. 101, Release 4-80. Washington, D. C.: U. S. Department of Interior, Fish and Wildlife Service, Division of cal Services.

Black-Tailed Prairie Dog Status and Future Conservation Planning

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Abstract.-The black-tailed prairie dog is one of five prairie dog species estimated to have once occupied up to 100 million ha or more in North America. The area occupied by black-tailed prairie dogs has declined to approximately 2% of its former range. Conversion of habitat to other land uses and widespread prairie dog eradication efforts combined with sylvatic plague, Yersinia pestis, have caused significant reductions. Although, the species itself is not in imminent jeopardy of extinction, its unique ecosystem is jeopardized by continuing fragmentation and isolation.

INTRODUCTION

The black-tailed prairie dog, Cynomys *ludovicianus* Ord, is the most widespread and abundant of five species of prairie dog in North America. Two species, the Utah prairie dog, C. *parvidens* J.A. Allen and the Mexican prairie dog, C. *mexicanus,* are currently listed as threatened and endangered, respectively, under the Endangered Species Act of 1973. The two other widespread species are the white-tailed prairie dog, C. *leucurus* Merriam and the Gunnison's prairie dog, C. *gunnisoni* Baird.

The black-tailed prairie dog is native to the short and midgrass prairies of North America. Its historic range stretches from southern Canada to northern Mexico and includes portions of Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming (Hall and Kelson 1959). The eastern boundary of prairie dog range is approximately the western edge of the zone of tallgrass prairie, from which prairie dogs are ecologically excluded. The western boundary of this species is roughly the Rocky Mountains. Its range is contiguous with, but generally does not overlap, ranges of other prairie dog species.

With the exception of Arizona, from which it has been extirpated, the species still occurs in all the states (including Canada and Mexico) within its historic range. Yet, widespread reductions have occurred in population numbers and occupied areas throughout this broad range. Historic evidence suggests that the total area occupied by all species of prairie dogs may have declined by as much as 98% during the first half of this century (Miller et al. 1994).

METHODS

We sent letters of inquiry to state and federal conservation and land management agencies and consulted published reports. This information was augmented by telephone interviews with individuals knowledgeable about prairie dog management. The area surveyed included all states within the original range of the black-tailed prairie dog. Although responses were received from all states and agencies queried, the quality of survey information varied. Therefore, this report is a picture of prairie dogs in the mid-1980s rather than an accurate assessment of 1995 populations.

Prairie dog abundance and distribution is probably better documented at present than at any previous time due to improved mapping techniques and greater interest in prairie dogs by land management agencies. Yet, prairie dog occupied acreage can still only be grossly estimated. A primary factor contributing to this uncertainty is that much of the mapping effort is temporally distributed over a decade or more and there is no method available to assess prairie dog abundance over a broad area within a short span of time. Typically, prairie dog populations change substantially within a few years due to the threats discussed below and to climatic factors and prairie dog reproductive ecology. Another factor contributing to errors in determining prairie dog abundance is a lack of information from private and state lands.

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THREATS TO THE PRAIRIE DOG

A number of causes have been identified or proposed to account for the reductions in the acreage occupied by black-tailed and other prairie dog species. We believe that four areas of threat warrant further discussion: 1) loss of habitat due to conversion of prairie to other land uses; 2) intentional poisoning or other eradication or control efforts, primarily prompted by the livestock industry; 3) shooting for recreation or as a control effort; and 4) sylvatic plague, *Yersinia pestis.*

LOSS OF PRAIRIE

Prairie dominated by blue grama, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths, and buffalograss, *Buchloe dactylides* (Nutt.) Engelm., possibly due to its relatively flat topography, is among the first grassland converted to.agriculture (Dinsmore 1983). As a result, Graul (1980) noted that as much as 45% of this prairie type has been lost to other land uses. Reductions in all shortgrass and midgrass prairies is expected to be similar or possibly greater in some midgrass regions where precipitation may be more suitable for agriculture. Although National Grassland acreage in the northcentral region of the Forest Service represents only about 5% of that agency's land base, it also represents the majority of the native prairie remaining in this region of North and South Dakota (Knowles and Knowles 1994).

Currently, with the exception of some areas of the northwestern portion of the black-tailed prairie dog's range, conversion of prairie to agricultural has lessened. This is because much of the arable land is already in cultivation or has been converted to non-native grasses for forage. Municipal and industrial development probably account for most of the present losses to native prairies in the United States. While these losses are minor compared with those that occurred during settlement of this country, they continue to reduce habitat availability for prairie dogs and other species.

ERADICATION OR CONTROL EFFORTS

Eradication efforts have been carried out against prairie dogs on a very large scale, affecting several million ha of land (Anderson et al. 1986; Bell 1921). Clark (1979) reported that in some years prairie dogs were intentionally poisoned on more than 8 million ha in the United States. During the early 1980s, 185,600 ha of prairie dogs were eradicated on the Pine Ridge Indian Reservation in South Dakota (Hanson 1988; Sharps 1988). In 1986 and 1987, a South Dakota black-tailed prairie dog complex of 110,000 ha was destroyed, eliminating the largest remaining complex in the United States (Tschetter 1988).

Virtually every federal land management agency has been involved in this effort. The U.S. Fish and Wildlife Service used compound 1080 until its ban in 1972. In 1976, this agency approved the use of zinc phosphide as a prairie dog control agent, hoping to avoid secondary poisoning of nontarget species while maintaining its prairie dog poisoning program. It is estimated that permitting activities by both the Environmental Protection Agency and the Animal and Plant Health Inspection Service account for the annual poisoning of 80,000 ha of prairie dogs in the United States (Captive Breeding Specialist Group 1992). Much of this effort occurs on federally-owned and managed land, despite the fact that less than 5% of the United States beef weight is produced on these lands (United States General Accounting Office 1988). Most poisoning on federal land is due to private land concerns, not necessarily federal forage concerns.

The legal designation indicating the regulatory status of the black-tailed prairie dog varies among the 10 states in which it still occurs. In four states the species is designated a legal agricultural pest, with some level of either state or local mandatory controls in effect. This includes statewide legislation mandating control of prairie dogs in Wyoming. In Colorado, Kansas, and South Dakota, state legislation allows counties or townships to mandate controls on landowners. In 1995, Nebraska repealed their long-standing legislation that mandated statewide control, thereby joining the states of Montana, New Mexico, North Dakota, Oklahoma, and Texas, where control is not mandatory but assistance may be provided to landowners who believe they have a prairie dog population problem that requires control.

PRAIRIE DOG SHOOTING

Shooting of prairie dogs, either for recreation or to reduce or control their numbers, is widespread across the range of all species in the United States.

The impact this activity has on overall populations remains unclear, but preliminary monitoring results by the Bureau of Land Management (BLM) in Montana indicate that some level of shooting might impact the growth and expansion of prairie dog colonies (Reading et al. 1989). Fox and Knowles (1995) suggested that persistent unregulated shooting over a broad area of the Fort Belknap Indian Reservation in Montana might have significantly influenced prairie dog populations. However, they further concluded that it would require approximately one recreational day of shooting for every 6 ha of prairie dogs to result in such an impact. This level of shooting pressure is unlikely over the hundreds of thousands of ha of currently occupied range.

SYLVATIC PLAGUE

Prairie dogs have coexisted with a variety of predators for many centuries on the plains and have adapted means of persisting in spite of this predation. However, a more recent threat has arrived to which the prairie dog has no adaptive protection. A flea-borne bacterium, the sylvatic plague, was introduced into North America just before the turn of the century. First discovered in black-tailed prairie dogs in Texas in the 1940s (Cully 1989), small rodents such as prairie dogs apparently have no natural immunity to the plague, which now occurs virtually throughout the range of the black-tailed prairie dog.

The impacts of plague are more adverse than just the killing of many individuals. The plague persists in a colony resulting in a longer population recovery time than is common in colonies that have been poisoned (figure 1). Four years following impact, plague-killed colonies on the Rocky Mountain Arsenal National Wildlife Refuge had recovered to only 40%, while poisoned colonies had recovered to over 90% (Knowles 1986). Knowles and Knowles (1994) suggested that prairie dogs have survived the introduction of this disease simply due to their large, highly dispersed populations. Further reductions in these populations could make prairie dogs much more susceptible to local or regional extirpations due to the plague.

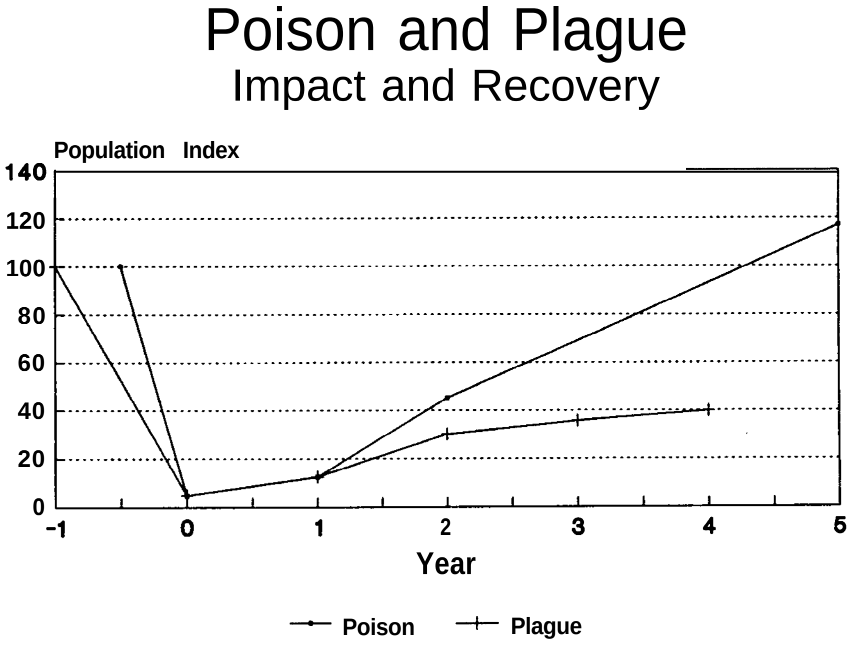

Figure 1. Comparison of prairie dog population recovery at the Rocky Mountain Arsenal National Wildlife Refuge following plague and at two colonies following control with zinc phosphlde (Knowles 1986).

HISTORIC AND CURRENT STATUS

Rangewide

Seton (1929) estimated that in the early part of this century, there may have been 5 billion prairie dogs in North America. Around that time, prairie dog colonies were estimated to occupy 40 million to 100 million ha of prairie in North America, but by 1960 this area was reduced to approximately 600,000 ha (Anderson et al. 1986; Marsh 1984). These estimates result in the often-cited figure of a 98% decline in population among the five species of prairie dog. So, while the black-tailed prairie dog still occurs in all but one of the states in its historic range, significant reductions in its total colony area have taken place rangewide.

Table 1. Historic 920) and recent (post-1980) estimates of total area (ha) occupied by black-tailed prairie dogs in the United States.

State	Historic	Recent	% Chancre
AZ	[1]	extirpated	-100
CO	2,833,000		
KS	810,000	18,845	-98
MT	595,000	35,545	-94
NE		24,415	[1]
NM[2]	4,838,460	201,220	-96
ND	85,000	8,500	-90
OK		3,850	[1]
SD	711,000	100,000	-86
TX	23,000,000	12,145	-99.9
WY		82,590	-75
United States	40,000,000 to 100.000.000	550,000	-98 to -99

[1] *Reliable data unavailable for analysis.*

[2] *Includes black-tailed and Gunnison's prairie dogs.*

PRAIRIE DOG STATUS IN EACH STATE

Current status information was solicited from state and federal agencies and from tribal authorities in all eleven states in the historic range of the black-tailed prairie dog (table 1). The following summary provides updated status and population data for those states.

Arizona

The Arizona Game and Fish Department (Duane L. Shroufe, Director, *in litt.* 1995) confirms that the black-tailed prairie dog, in the form of the Arizona subspecies C. *ludovicianus arizonensis*, is extirpated from the state. However, it still occurs nearby in Mexico and New Mexico. Arizona still supports populations of Gunnison's prairie dogs.

Colorado

On the Comanche and Pawnee National Grasslands, the Forest Service *(in litt.)* currently estimates a total of 2,455 ha of active prairie dogs, compared with 910 ha from 1978 to 1980 (Schenbeck 1982). This represents more than a doubling in area, but also represents only 0.5% of the area available on these public lands. Bent's Old Fort National Historic Site contains 325 ha of black-tailed prairie dogs (NPS, *in litt.).* Fort Carson and surrounding private lands contain approximately 1,620 ha, Pinyon Canyon less than 810 ha of prairie dogs (FWS, *in litt.).* The Rocky Mountain Arsenal NWR (FWS, *in litt.)* prairie dog population declined from 1,850 ha to 100 ha between 1988 and 1989, due to plague. Burnett (1918) estimated that three combined species of prairie dog occupied 5,665,720 ha in Colorado in the early 1900s. Based on geographic distribution of black-tailed, white-tailed, and Gunnison's prairie dogs in the state, it may be assumed that black-tailed prairie dogs accounted for approximately half this figure. There is no reliable estimate of the total area occupied by black-tailed prairie dogs statewide at this time.

Kansas

The National Park Service *(in litt.)* reports approximately 16 ha of prairie dogs at the Fort Larned National Historic Site. On the Cimarron National Grassland, the Forest Service *(in litt.)* currently estimates 440 ha of active prairie dog colonies compared with 20 ha estimated from 1978 to 1980 (Schenbeck 1982). This represents more than a twenty-fold increase on this 44,000-ha area, yet still only 1% of the total area of the Grassland. Both Lee and Henderson (1988) and Powell and Robe1 (1994) reported that selected counties had reductions of 84% since the beginning of the century (Lantz 1903, cited in Lee and Henderson 1988). A survey completed in 1992

(Vanderfoof et al. 1994) estimates 18,845 ha of prairie dogs in Kansas, just over 2% of the 810,000 ha estimated by Lantz (1903) some 90 years ago.

Montana

Flath and Clark (1986) estimated that black-tailed prairie dogs occupied 595,000 ha of land in Montana from 1908 to 1914. Estimated prairie dog occupied area by the early 1980s had declined to 50,600 ha (Flath and Clark 1986) and subsequent estimates show further declines in prairie dogs (40,500 ha, Campbell 1986; 35,545 ha, FaunaWest Wildlife Consultants 1995). This most recent estimate indicates a statewide reduction in occupied area of approximately 94% since the early 1900s.

Nebraska

On the Oglala National Grassland and Nebraska National Forest, the Forest Service *(in litt.)* currently estimates 105 ha of active prairie dog colonies, compared with 145 ha estimated from 1978 to 1980 (Schenbeck 1982). Current estimates represent 1.4% of land available. In 1973, prairie dog occupied area in Nebraska was estimated at 6,075 ha (Lock 1973). By 1982, this figure had increased to an estimated 32,400 ha (Frank Andelt, Nebraska Game and Parks Commission, cited in FaunaWest Wildlife Consultants 1995). By 1989, prairie dogs statewide occupied approximately 24,415 ha (Kevin Church, Nebraska Game and Parks Commission, *in litt.).* Plague and increased eradication efforts, resulting from state legislation mandating prairie dog control, have reduced this figure significantly since the 1980s, with less than 0.22% of the Nebraska landscape currently occupied by the species (FaunaWest Wildlife Consultants 1995). Historic estimates are unavailable.

New Mexico

The BLM *(in litt.)* reports that prairie dogs may be extirpated from several sites, with only 140 ha remaining on BLM land in the state. The White Sands Missile Range (Department of Army, *in litt.)* contains just over 300 ha of prairie dogs. Around 1919 the area in New Mexico occupied by prairie dogs, both Gunnison's and black-tailed (including C. *l. arizonensis),* was approximately 4,838,460 ha, but was estimated to have been reduced to 201,220 ha by 1980 (Hubbards and Schmitt 1984). This is a 96% reduction. Hubbards and Schmitt (1984) further estimated that the range of the black-tailed prairie dog in New Mexico has been reduced by one-fourth, primarily from the range of *arizonensis.*

North Dakota

Theodore Roosevelt National Park reportedly contains less than 360 ha of prairie dogs (NPS, *in litt.),* approximately 1% of the total Park land area. There are believed to be currently 2,690 ha of prairie dogs on the 660,435 ha of Custer National Forest in North and South Dakota (Forest Service, *in litt.).* This represents 0.4% prairie dog occupancy of these lands. The Forest management plan calls for an occupancy level at or around 2,225 ha. The North Dakota Game and Fish Department *(in litt.)* reports approximately 8,300 ha of prairie dogs statewide, which may be a reduction of 90% or more from historic levels. In 1992, only six complexes of over 400 ha were identified.

Oklahoma

The Department of the Army *(in litt.)* has no current estimate of prairie dog areas on Fort Sill, but report that they have declined markedly in the past 10 years. Shackford et al. (1990) reported a statewide estimate of 3,850 ha in 1967, increasing by 93% to 7,440 ha in 1989.

South Dakota

On the Buffalo Gap and Fort Pierre National Grasslands, the Forest Service *(in litt.)* estimates 3,025 ha of active prairie dog colonies and an additional 2,600 ha of colonies are subject to periodic rodenticide treatments. This compares to 17,600 ha estimated from 1978 to 1980 (Schenbeck1982). The 500,285 ha Black Hills National Forest and Custer and Elk Mountain Ranger Districts currently support 53 ha of prairie dogs. In the early 1920s there may have been 711,000 ha of prairie dogs statewide (FaunaWest Wildlife Consultants 1995). The South Dakota Animal Damage Control office currently estimates 80,000 to 100,000 ha of active prairie dog colonies in the state; the Bureau of Indian Affairs estimates 65,000 ha of these on tribal lands (Cheyenne River Sioux Tribe, *in litt.).* These estimates suggest at least an 86% decline in prairie dog occupied area across the state.

lands and Wind Cave National Parks currently contain 1,660 and 3,085 ha of prairie dogs, respectively (NPS, *in litt.).* These numbers represent 2 and 4% respectively, of the area available on these public lands.

Texas

There were an estimated 31,385 ha of prairie dogs in northwest Texas in 1973 (Cheatham 1973). In 1991, there were at least 12,145 ha of prairie dogs estimated in Texas (Peggy Horner, Texas Parks and Wildlife, *in litt.).* Comparing this with a statewide historic estimate of 23,000,000 ha (Merriam 1902) results in a decline of over 99% in this century.

Wyoming

On Thunder Basin National Grassland, the Forest Service *(in litt.)* currently estimates 1,500 ha of active prairie dog colonies, with an additional 4,900 ha subject to periodic rodenticide treatment. Colony area for the period 1978 to 1980 was reported to be 2,550 ha (Schenbeck 1982). These numbers represent 0.6% of this 231,500 ha public grassland area. Devil's Tower National Monument contains approximately 16 ha of black-tailed prairie dogs (NPS, *in litt.);* 3% of the area available. Black-tailed prairie dogs in Wyoming may have increased in abundance near the turn of the century as a result of sheep and cattle grazing, with an estimated 53,650 ha by 1971 (Clark 1973). However, Campbell and Clark (1981) estimated a 75% reduction in prairie dog occupied areas since 1915. Current estimates indicate between 53,000 and 82,590 ha statewide (Wyoming Game and Fish Department, cited in FaunaWest Wildlife Consultants 1995).

SUMMARY OF PRAIRIE DOG STATUS IN EACH STATE

FaunaWest Wildlife Consultants (1995) attempted to estimate the amount of land area within the range of the black-tailed prairie dog that is currently occupied by the species. They included seven Great Plains states in their analysis and concluded that the states have less than a 1% occupancy of land surface within the species' range. The states included in this assessment and the percent of prairie dog occupancy within available area are Colorado (0.35%), Kansas (0.14%), Montana (0.17%), Nebraska (0.22%), North Dakota (0.17%), South Dakota (0.80%), and Wyoming (0.60 to 0.88%).

While these individual state accounts do not represent an exhaustive rangewide status review, they unfortunately provide the best information available. Significant reductions in occupied area have and continue to occur throughout the species' range; losses in some places exceeded 95%. Although the species still occurs in all but one state in its historic range, the eastern boundary of this distribution may be receding to the west. Figures indicate that there may be more than 550,000 ha of occupied black-tailed prairie dog range remaining in the United States, which is consistent with the estimate of 600,000 ha (Marsh 1984) cited previously. Over half the known prairie dog acreage in the central and northern Great Plains occurs on private land, almost 30% is on Indian reservations, and about 6% each occurs on Forest Service and Bureau of Land Management property (figure 2, FaunaWest Wildlife Consultants 1995). Neither Park Service nor Fish and Wildlife Service lands support significant acreage of any prairie dog species.

There is a need to develop a standardized survey technique for assessing prairie dog status. Presently, two methods are commonly employed and both involve mapping of individual prairie dog colonies either by ground reconnaissance or from aerial photo interpretation. Both methods are time consuming and expensive, making it unreasonable to expect a survey of over 500,000 ha of prairie dog colonies on the Great Plains within a short time period. Prairie dog colonies represent clumped patches on a broad landscape and there already exist nonmapping techniques that might be capable of statistical sampling of this distribution (Marcum and Loftsgaarden 1980). A statistical approach to monitoring prairie dog colony acreage may be a more appropriate technique than trying to map all prairie dog colonies.

PRAIRIE DOGS AND LIVESTOCK

Efforts to eradicate the prairie dog by the livestock and agricultural industry have existed for most of this century. Merriam (1902) estimated that prairie dogs caused a 50 to 75% reduction in range productivity. Taylor and Loftfield (1924) concluded that the prairie dog is"one of the most injurious rodents of the

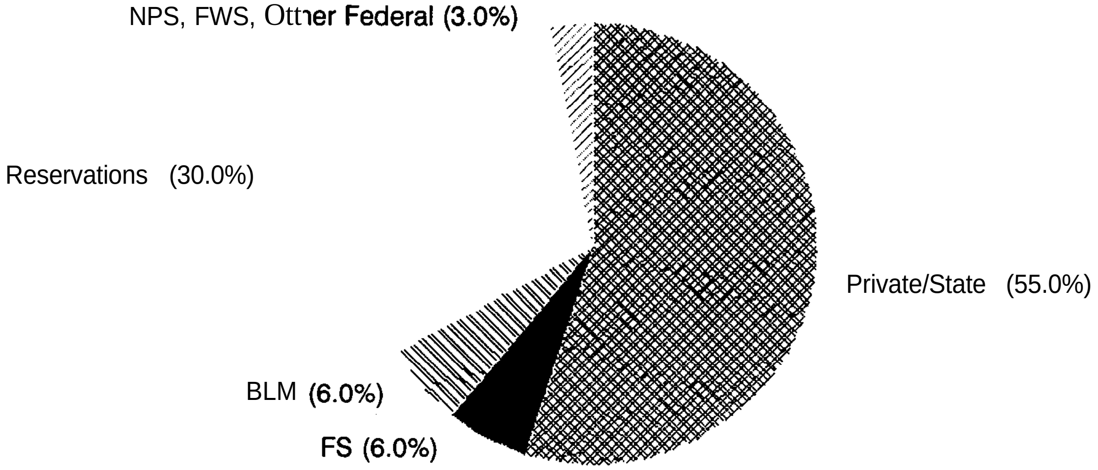

Figure 2. Distribution of black-tailed prairie dog colonies by land ownership in seven states in the northern and central Great Plains.

southwest and plains regions," and results in "the removal of vegetation in its entirety from the vicinity." Reports such as these were largely responsible for the escalating effort by range managers on the Great Plains to eradicate the prairie dog.

The conflict between the livestock industry and the prairie dog will likely not end easily or quickly, despite reports that prairie dog foraging does not significantly affect weight gain of cattle (O"Meilia et al. 1982; Hansen and Gold 1977). Others have reported the beneficial effects of prairie dogs on long-term range condition, including increased plant species diversity, richness, and overall plant production in prairie dog colonies (Archer et al. 1987; Uresk and Bjugstad 1983; Bonham and Lerwick 1976; Gold 1976). Uresk (1985) demonstrated that up to four years following prairie dog control, plant production was not increased whether the range was grazed or ungrazed by cattle.

Conversely, Hanson and Gold (1977) reported dietary overlap between cattle and prairie dogs, suggesting there may be some competition for the same species of forage plants. An estimation of true competition would be dependent on a variety of factors, including density of prairie dogs, stocking rate of cattle, ground cover, forage species present, and others (Uresk and Paulson 1988). Collins et al. (1984) reported that the annual cost of prairie dog poisoning was higher than the annual value of the forage gained by these measures. This issue requires more study, with input from both sides of the debate.

PRAIRIE DOGS AND BIODIVERSITY

The prairie dog, an integral component of the shortgrass prairie biotic community, is capable of transforming its own landscape and creating habitat alterations on a scale surpassed only by humans on the Great Plains. The ecosystem that is maintained by the prairie dog is valuable to many other species, with over 100 species of vertebrate wildlife reportedly using prairie dog colonies as habitat (Sharps and Uresk 1990; Clark et al. 1989; Reading et al. 1989). While few of these species are critically dependent on prairie dogs for all their life requisites, the increased biodiversity associated with prairie dog colonies indicates the importance of this habitat. Agnew et al. (1986) reported greater avian densities and species richness on prairie dog colonies. Also, numerous researchers have documented the preferential feeding of wild and domestic ungulates on prairie dog colonies (Coppock et al. 1983; Detling and 1987; Knowles 1986; Krueger 1986; Wydeven and Dahlgren 1985).

A number of rare and declining species are associated with prairie dogs and the habitat they provide. The black-footed ferret, *Mustela nigripes* Audubon and Bachman, 1851, is considered a true prairie dog obligate because it requires the prairie dog ecosystem for its survival. As one of the most endangered mammals in North America, this species has come to symbolize the decline in native grassland biodiversity. At least two species that are candidates for listing under the Endangered Species Act are also associated to a lesser degree with prairie dogs. The mountain plover, *Charadrius montanus* Townsend, 1837, and the swift fox, *Vulpes velox* Say, *1823,* are attracted to the vegetative changes and possibly increased food availability in prairie dog colonies. The association of other species that are either declining or vulnerable indicate the problems facing this habitat.

CONSERVATION EFFORTS

Prairie dogs are managed either directly or indirectly within the survey area by at least six federal agencies, 11 state wildlife departments, state agriculture departments, departments of state lands, and numerous weed and pest districts, counties and private landowners. Prairie dog management goals and objectives vary significantly among these entities. Even management within agencies but between areas varies significantly. This variation can range from total protection of prairie dogs to a legal mandate to exterminate. All states have simultaneously classified the prairie dog as a pest and as wildlife, often with opposing management goals. Federal policy regarding prairie dogs has been inconsistent over time and across geographic regions. The legal mechanisms responsible for the decline of prairie dogs during this century are still intact. Restoration of the prairie dog ecosystem may not be possible without major changes in management policy.

At least two federal agencies have taken the initiative to begin to address the problems associated with declining prairie dog occupied areas and to involve other interested parties. The Forest Service initiated a working group comprised of various federal land and resource agencies throughout the northern states in the Great Plains, involving the Bureau of Land Management, Park Service, Bureau of Indian Affairs, and Fish and Wildlife Service. The function of this group is to encourage development of conservation assessments and strategies for the species across broad landscapes.

In January 1995, the Fish and Wildlife Service convened a meeting of federal, state, and nongovernmental entities to discuss problems facing the shortgrass prairie ecosystem, including the prairie dog as a focal species. Consensus recommendations were: 1) Fish and Wildlife Service will develop conservation strategies to keep prairie species from becoming listed under the Endangered Species Act and to recover declining species before a listing occurs; and 2) work with the Western Governor's Association to investigate ways to coordinate and communicate with all involved parties on prairie issues. The Fish and Wildlife Service recognizes that prairie dog management remains within the jurisdiction of the various state and federal land management agencies. Therefore, this agency is particularly interested in participating in cooperative agreements with other agencies so that the prairie dog may be managed as a wildlife species rather than simply controlled as a pest.

CONCLUSION

The black-tailed prairie dog does not appear to be in danger of becoming extinct in the foreseeable future, given current management. However, the additional negative impacts resulting from habitat fragmentation (Wilcox and Murphy 1985) could seriously impact the ability of some prairie dog populations to persist or become re-established. Habitat fragmentation adversely quickly affects highly specialized species (Miller et al. 1994) and the myriad of species associated with prairie dog colonies recover from habitat or population losses at different rates. This could result in a significant disruption of the ecosystem overall functioning, further delaying its recovery. Such effects are already evident for the endangered black-footed ferret. The future recovery or extinction of this species is inextricably entwined with the decisions resource managers make today regarding the conservation of the prairie dog ecosystem.

Management of the black-tailed prairie dog must give greater consideration to developing an abundance and distribution of prairie dogs that will ensure long-term population persistence of associated species. As a minimum, we believe that broad areas of suitable grasslands should have from 1 to 3% of the area occupied by prairie dogs. Federally-owned lands should assume a greater share of this responsibility, with a goal of from 5 to 10% occupancy by prairie dogs. Maintaining this level of occupancy may allow resource managers to determine what actually constitutes a functioning prairie dog ecosystem, so attempts may be made to preserve this system into the future.

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LITERATURE CITED

Agnew, W.,D.W. Uresk, and R.M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent mixed-grass prairie in western South Dakota. J. Range Manage. 39:135-139.

Anderson, E., S.C. Forrest, T.W. Clark, and L. Richardson. 1986. Paleo-biology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* Audubon and Bachman (1851). Great Basin Naturalist Memoirs 8:11-62

Archer, S. M.G. Garrett, and J.K Detling. 1987. Rates of vegetation change associated with prairie dog grazing in North American mixed-grass prairie. Vegetatio 72:159-166

Bell, W.R. 1921. Death to the rodents. U.S. Dept. of Agric. Yearbook 1920:421-438.

Bonham, C.D. and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. J. Range Manage. 29:221-225.

Burnett, W.L. 1918. Rodents of Colorado in their economic relation. Office of State Entomology, Colorado Agric. Coll., Fort Collins, CO. Circ. 25:1-31.

Campbell, T.M. III. 1989. Prairie dog colony location surveys and black-footed ferret searches in Montana. Pages l-12 *in* T.W. Clark, D. Hinckley, and T. Rich, eds., The prairie dog ecosystem: managing for biological diversity. MT BLM Wildlife Technical Bull. No. 2.

Campbell, T.M. III and T.W. Clark. 1981. Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. Amer. Mid. Nat. 105:269-276.

Captive Breeding Specialist Group. 1992. Black-footed ferret recovery plan review, Washington, DC, 22-24 July. Captive Breeding Specialist Group, Apple Valley, MN. 43 pp.

Cheatham, L.K. 1973. Censusing prairie dog colonies using aerial photographs. Pages 77-88 *in* R.L. Linder and C.N. Hillman, eds. Black-footed ferret and prairie dog workshop. SD State Univ., Brookings, SD.

Clark, T.W. 1973. Prairie dogs and black-footed ferrets in Wyoming. Pages 88-101 *in* R.L. Linder and C.N. Hillman, eds. Black-footed ferret and prairie dog workshop. SD State Univ., Brookings, SD.

Clark, T.W. 1979. The hard life of the prairie dog. National Geographic 156(2):270-281.

Clark, T.W., D. Hinckley, and T. Rich, eds. 1989. The prairie dog ecosystem: managing for biological diversity. MT BLM Wildlife Technical Bull. No. 2.

Collins, A.R., J.P. Workman, and D.W. Uresk. 1984. An economic analysis of black-tailed prairie dog control. J. Range Manage. 37:358-361.

Coppock, D.L., J.K. Detling, J.E. Ellis, and M.I. Dyer. 1983. . Plant herbivore interactions in a mixed grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1-9.

Cully, J.F., Jr. 1989. Plague in prairie dog ecosystems: importance for black-footed ferret management. In T.W. Clark, D. Hinckley, and T. Rich, eds., The prairie dog ecosystem: managing for biological diversity. MT BLM Wildlife Technical Bull. No. 2.

Detling, J.K. and A.D. Whicker. 1988. A control of ecosystem processes by prairie dogs and other grassland herbivores. Pages 23-29 *in* Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Rapid City, SD. U.S. Forest Service, Washington, DC.

Dinsmore, J.J. 1983. Mountain plover *(Charadrius montanus).* Pages 185-196 *in* Armbruster, J.S., ed. Impacts of coal surface mining on 25 migratory birds of high federal interest. U.S. Fish and Wildlife Service. FWS/OBS-83/35/

FaunaWest Wildlife Consultants. 1995. A summary of black-tailed prairie dog abundance and distribution on the central and northern Great Plains. Report prepared for Defenders of Wildlife, Missoula, MT. 46 pp. + app.

Flath, D.L. and T.W. Clark. 1986. Historic status of black-footed ferret habitat in Montana. Great Basin Nat. Mem. 8:63-71.

Fox, M. and C. Knowles. 1995. Economic and ecological evaluation of the Fort Belknap Indian Reservation fish and wildlife program. Poster presentation at MT Chapter of TWS, 31 Jan-l Feb, 1995, Billings, MT.

Gold, I.K. 1976. Effects of black-tailed prairie dog mounds on shortgrass vegetation. M.S. Thesis, CO State Univ., Fort Collins, CO. 39 pp.

Graul, W.D. 1980. Grassland management practices and bird communities. Pages 38-47 *in* DeGraff, R.M., Technical Coordinator. Management of western forests and grasslands for nongame birds. U.S. Forest Service. GTR INT-86.

Hall, E.R. and K.R. Kelson. 1959. The mammals of North America. Ronald Press, New York, NY.

Hanson, R. 1988. A Chronology of prairie dog control operations and related developments in South Dakota. Pages 121-122 *in* Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Rapid City, SD. U.S. Forest Service, Washington, DC.

Hanson, R.M. and I.K. Gold. 1977. Black-tailed prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. J. Range Manage. 30:210-214.

Hubbard, J.P. and C.G. Schmitt. 1984. The black-footed ferret in New Mexico. Endangered Species Program, Dept. of Game and Fish, Santa Fe, NM.

Knowles, C.J. 1986. Some relationships of black-tailed prairie dogs to livestockgrazing. Great Basin Nat. 46:198-203.

Knowles, C.J. and P.R. Knowles. 1994. A review of black-tailed prairie dog literature in relation to rangelands administered by the Custer National Forest. U.S. Forest Service. 61 pp.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecology 67:760-770.

Lantz, D.E. 1903. Destroying prairie dogs and pocket gophers. KS State Agric. College Bull. No. 116.

Lee, C.D. and R.F. Henderson. 1988. Kansas attitudes on prairie dog control. Pages 162-165 *in* Ninth Great Plains Wildlife Damage Control Workshop Proc.

Lock, R.A. 1973. Status of the black-footed ferret and black-tailed prairie dog in Nebraska. Pages 44-46 *in* R.L. Linder and C.N. Hillman, eds. Black-footed ferret and prairie dog workshop. SD State Univ., Brookings, SD.

Marcum, C.L. and D.O. Loftsgaarden. 1980. Anonmapping technique for studying habitat preferences. J. Wildl. Manage. 44:963-968.

Marsh, R.E. 1984. Ground squirrels, prairie dogs and marmots as pests on rangeland. Pages 195-208 *in* Proceedings of the conference for organization and practice of vertebrate pest control, Hampshire, England. Plant Protection Division, Fernherst, England.

Merriam, C.H. 1902. The prairie dog of the Great Plains. Pages 257-270 *in* Yearbook of the U.S. Dept. of Agric. 1901. U.S. Government Printing Office. Washington, DC.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8(3):677-681

O'Meilia, M.E., F.L. Knopf, and J.C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. J. Range Manage. 35:580-585.

Powell, K.L. and R.J. Robel. 1994. Size and location of black-tailed prairie dog towns in Meade and Gray Counties, Kansas. Trans. KS Acad. Sci. 97:44-49.

Reading, R.P., J.J. Grenston, S.R. Beissinger, and T.W. Clark. 1989. Attributes of black-tailed prairie dog colonies in north-central Montana, with management recommendations for the conservation of biodiversity. Pages 13-28 *in* T.W. Clark, D. Hinckley, and T. Rich, eds., The prairie dog ecosystem: managing for biological diversity. MT BLM Wildlife Technical Bull. No. 2.

Schenbeck, G.L. 1982. Management of black-tailed prairie dogs on the National Grasslands. Pages 207-217 in Fifth Great Plains Wildlife Damage Control Workshop Proc.

Seton, E.T. 1929. Lives of game animals. Doubleday, Dovan, and Co., Inc., Garden City, NY. 949 pp.

Shackford, J.S., J.D. Tyler, and L.L. Choate. 1990. A survey of the black-tailed prairie dog in Oklahoma. Final report submitted to OK Dept. of Wildlife Conservation. Cameron Univ., Lawton, OK. 18 pp.

Sharps, J.C. 1988. Politics, prairie dogs, and the sportsman. Pages 117-118 *in* Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Rapid City, SD. U.S. Forest Service, Washington, DC.

Sharps, J.C. and D.W. Uresk. 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. Great Basin Nat. 50:339-345.

Taylor, W.P. and J.V.G. Loftfield. 1924. Damage to range grasses by the Zuni prairie dog. U.S. Agric. Bull. 1227.

Tschetter, B.J. 1988. Estimates of South Dakota prairie dog acreages, 1987. Report No. 88.01. SD Dept. of Game, Fish and Parks, Pierre, SD.

U.S. General Accounting Office. 1988. More emphasis needed on declining and overstocked grazing allotments. GAO/RCED-88-80. Washington, DC.

Uresk, D.W. 1985. Effects of controlling black-tailed prairie dogs on plant production. J. Range Manage. 38:466-468.

Uresk, D.W. and A.J. Bjugstad. 1983. Prairie dogs as ecosystem regulators on the northern high plains. Pages 91-94 *in* Seventh North American Prairie Conference Proceedings, Southwest Missouri State Univ., Springfield, MO.

Uresk, D.W. and D.D. Paulson. 1988. Estimated carrying capacity for cattle competing with prairie dogs and forage utilization in western South Dakota. Pages 387-390 *in* Symposium on Management of Amphibians, Reptiles, and Small Mammals in North America. Flagstaff, AZ.

Vanderhoof, J.L., R.J. Robel, and K.E. Kemp. 1994. Numbers and extent of black-tailed prairie dog towns in Kansas. Trans. KS Acad. Sci. 97:36-43.

Wilcox, B.A. and D.D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. Amer. Nat. 125:879-887.

Wydeven, A.P. and R.B. Dahlgren. 1985. Ungulate habitat relationships in Wind Cave National Park. J. Wildl. Manage. 49:805-813.

The Role of Fire in Managing for Biological Diversity on Native Rangelands of the Northern Great Plains

Carolyn Hull Sieg[1]

Abstract.-A strategy for using fire to manage for biological diversity on native rangelands in the Northern Great Plains incorporates an understanding of its past frequency, timing and intensity. Historically, lightning and humans were the major fire setters, and the role of fire varied both in space and time. A burning regime that includes fires at various intervals, seasons and intensities, including midsummer burns, should be reinstated. However, burning to enhance rare systems and species and to discourage exotic species is also needed. The goal is to base plans on an understanding of historic processes and ecosystem interactions, and resist techniques that rely on unexamined conventions.

INTRODUCTION

"A common thread runs through the many definitions of biological diversity: variety of life and its processes in a given area" (Salwasser 1990). A management strategy for conserving biological diversity of any natural ecosystem must focus on saving all the components, including the structure, composition (including genetic diversity), and processes that characterize these systems (Kaufmann et al. 1994). Biological diversity is more than just the identifiable parts; it also includes the symbioses and synergisms that make nature work (Salwasser 1990).

The importance of disturbances in shaping native communities has recently received more attention. Ecosystems are dynamic entities whose patterns and processes are shaped and sustained on the landscape by successional processes and by abiotic disturbances such as fire, drought, and wind. To sustain these ecosystems, processes that characterize the variability found in native ecosystems should be present and functioning, and management activities should conserve or restore historic disturbance patterns (Kaufmann et al. 1994). This paper describes a strategy for managing biological diversity of rangelands on the Northern Great Plains. The approach is based on restoring historical disturbance processes given the significantly altered landscape patterns of today. Plant nomenclature follows Great Plains Flora Association (1986) (table 1).

SETTING

The Northern Great Plains region includes North Dakota, South Dakota and Nebraska, plus the eastern portions of Montana and Wyoming, and extends northward into Manitoba, Saskatchewan and Alberta. The climate of the region is characterized by an increase in precipitation and humidity and a decrease in periodic droughts during the summer from west to east (Risser 1990). This climate range influences not only the potential native vegetation but also the fire regime and effects. The shortgrass prairie on the Western and Southern portions of the region is the most arid type; the mixed-grass prairie occurs in the midsection of the region; and the tallgrass prairie on the Eastern edge receives the most precipitation (Risser et al. 1981).

The variation in precipitation across the region greatly influences the growth and expansion of woody plants. In the most Western portion of the region, big sagebrush occupies uplands; in the absence of fire it persists or expands (Wright and Bailey 1982). In the remainder of the shortgrass and mixed-grass portions of the region, woody plants are restricted to areas of increased elevation, such as the Black Hills, or to areas of increased moisture such as riparian zones, draws, and north-facing slopes. Escarpments, ridges, and outcrops in the Western portion support
rosa pine and Rocky Mountain juniper (Wells 1965).

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Table 1. Common and scientific names used in this report. Nomenclature follows GreatPlains Flora Association (1986).

Common name	Scientific name
Graminoids	
big bluestem	*Andropogon gerardii*
smooth brome	*Bromus inermis*
cheatgrass	*Bromus tectorum*
Japanese brome	*Bromus japonicus*
buffalo grass	*Buchloe dactyloides*
threadleaf sedge	*Carex filifolia*
sand dropseed	*Sporobolus cryptandrus*
green needlegrass	*Stipa viridula*
Forbs	
leafy spurge	*Euphorbia esula*
western prairie fringed orchid	*Platanthera praeclara*
Shrubs and trees	
sagebrush	*Artemisia* spp.
dwarf sagebrush	*Artemisia cana*
big sagebrush	*Artemisia tridentata*
green ash	*Fraxinus pennsylvanica*
Rocky Mountain juniper	*Juniperus scopulorum*
Eastern red cedar	*Juniperus virginianus*
cactus	*Opuntia* spp.
ponderosa pine	*Pinus ponderosa*
plains cottonwood	*Populus deltoides*
aspen	*Populus tremuloides*
chokecherry	*Prunus virginiana*
bur oak	*Quercus macrocarpa*
willows	*Salix* spp.
snowberry	*Symphoricarpos occidentalis*

Woody draws (narrow woodlands occurring in ravines) are examples of communities in more arid portions of the region that are restricted to sites with greater soil moisture. The most common woody plants in these draws are green ash and chokecherry. Riparian zones along streams and rivers support plains cottonwood, willows, and dwarf sagebrush (Severson and Boldt 1978). These woodlands may also expand in the absence of fire, but the expansion is restricted to sites with adequate moisture and the expansion rate is slower than in the tallgrass region. Further, many deciduous species, such as chokecherry and willows, sprout vigorously following burning (Wright and Bailey 1982). Only very frequent fires (i.e., every 1 to 5 years) would favor grasses over these species.

In contrast to more arid portions of the region, mesic prairies in the Northern, Eastern and Southeastern portions of the region are characterized by precipitation amounts high enough to support the expansion of woody plants onto uplands. It is in these areas that frequent fires slow the expansionof woody plants on uplands (Bragg and Hulbert 1976). In the Northern portion of the region, aspen replaces ponderosa pine on outcrops and expands into the Canadian prairies (Wright and Bailey 1982). Eastern red cedar replaces Rocky Mountain juniper in the Southeastern part of the region where it readily expands onto uplands (Gehring and Bragg 1992). In the eastern tallgrass prairies, woody species, such as willows and bur oak, invade grasslands, and only frequent fires slow their expansion (Anderson 1990). Plains cottonwood and willow dominate floodplains in the more mesic portions of the Northern Great Plains; green ash and bur oak are common on higher terraces along major rivers (Johnson et al. 1976).

In addition to climatic factors, herbivores also influence the region's vegetation and fire regimes. However, it is difficult to distinguish the particular influence each force has on vegetation (Henderson and Statz 1995). Fire is often associated with periodic drought, and fire and grazing are sometimes interrelated. For example, recently burned grasslands often attract grazers; yet, heavily grazed areas usually resist fire until dead litter reaccumulates (Steuter et al. 1990, Vinton et al. 1993). Therefore, the influences of grazing and drought must be a part of a discussion of historical fire effects (Henderson and Statz 1995).

FIRE HISTORY

An understanding of the frequency, timing, and intensities of past fires is necessary before fire can be incorporated into a strategy to conserve prairie systems. Based on data from adjoining ponderosa pine forests, which indicated that fire frequency varied from 2 to 25 years, Wright and Bailey (1982) estimate that on level-to-rolling topography, a fire frequency of 5 to 10 years in the Northern Great Plains is reasonable. On topography more dissected with breaks and rivers, they estimate a fire frequency of 20 to 30 years. Wendtland and Dodd (1992) agree with this range, based on their examination of historical documents and fire records from the Scotts Bluff National Monument area in northwestern Nebraska. Dendrochronology data in the Devils Tower region northwest of the Black Hills reveal that before 1770 the mean interval between fires was 27 years; from 1770 to the fire return interval was 14 years (Fisher et al. 1987). Brown and Sieg (1996) report a mean fire frequency in the south-central Black Hills of 16 years for the period 1388 to 1918.

In the more mesic portions of the Northern Great Plains, the average fire return interval was shorter. Collins and Gibson (1990) estimate a frequency of every 1 to 5 years in the tallgrass portions of this region. In northcentral Nebraska, the fire return interval averaged 3.5 years between 1851 and 1900 (Bragg 1985).

Historically, the major ignition sources for prairie fires were lightning and American Indians. Lightning was, and is, an important ignition source in the Northern Great Plains. In northwestern South Dakota, lightning-set fires occur an average of 6 to 25 times per year, and most commonly occur in July and August (Higgins 1984); fewer occur in April, May, June, and September. Wendtland and Dodd (1992) note that of 10 fires described in historical documents between 1824 and 1934, and of 26 fires officially recorded between 1934 and 1969 in the Scotts Bluff National Monument area, over 70 percent occurred in July and August.

Higgins' (1986) review of 300 historical accounts written between 1673 and 1920 reveals that fires accidentally or intentionally set by American Indians were common in the Northern Great Plains. He found that although Indians set fires in nearly every month of the year, April, September and October were their peak fire-setting times. The majority of the 97 fires described were scattered, single events of short duration and small extent; only 10 fires burned longer than 1 day.

American Indians had many uses for fire. These included attracting and herding wild animals, signaling threats and warnings, improving pasturage, masking and eliminating personal signs at camps and along trails, and for pleasure, warfare and ceremonies (Higgins 1986). During their 10,000-year occupation of this region, the timing of fires set by American Indians did not mirror lightning-set fires; therefore, these Indian-set fires can be considered additive to lightning fires (Higgins 1986).

A combination of periodic droughts, high temperatures and strong winds in the region provide the components necessary for fire spread (Collins 1990). The end result of the erratic climate, flammable fuels, topographic relief and other factors, such as grazing animals, was that the role of fire was not constant in time or space (Anderson 1990).

With the arrival of non-native settlers came fire suppression policies and, in many areas, a shift in the timing of fires. Near Devils Tower, Wyoming, after 1900, the fire return interval increased to every 42 years, versus less than every 27 years previously (Fisher et al. 1987). In the south-central Black Hills, Brown and Sieg (1996) record a 104-year fire-free period in ponderosa pine stands between 1890 and 1994, and note that most of past fires occurred late in the growing season or after growth had ceased for the year. Higgins (1984) suggests that the recent extent and spread of lightning fires has been modified by cultural features such as roads; further, the fire regime has also been altered by differing patterns of grazing animals (first bison, then cattle). In contrast to the late summer ignitions that commonly burned before 1935 near Scotts Bluff, Nebraska, the 46 fires recorded since 1935 dramatically shifted to spring occurrences (Wendtland and Dodd 1992). Lengthening the interval between fires, shifting from summer to early spring burning, and/or reducing fire intensity by prescribing cooler fires may alter species composition to favor fire-intolerant species (Wendtland and Dodd 1992) such as cactus and non-sprouting woody species like sagebrush (Wright and Bailey 1982).

DEVELOPING A FIRE MANAGEMENT STRATEGY TO CONSERVE DIVERSITY

The fire strategy most likely to manage diversity on native rangelands of the Northern Great Plains is based on two premises: 1) processes that mimic, as much as possible, the variability found in native ecosystems should be present and functioning; and 2) management activities should conserve or restore historical disturbance patterns (Kaufmann et al. 1994). This management strategy should reflect the differing roles that fire historically played in the various portions of the region. However, this strategy must also address the fundamental changes that have occurred in the landscape such as drastically different landscape patterns imposed by species changes and management unit boundaries.

Wendtland and Dodd (1992) recommend a scenario that mimics the presettlement fire history. For the Scotts Bluff, Nebraska area, they infer this strategy including high intensity summer fires on a return interval of 5 to 30 years. Shifting burning programs from all spring or fall burns to include some midsummer burns should favor some species not enhanced by spring or fall burns (Howe 1994). For example, an April fire burns early foliage critical for root production of cool-season plants, leaving late-season plants unscathed; an August fire burns the largely inactive foliage of cool-season species, while consuming foliage and reproductive stems of warm-season species (Howe 1994). However, historically, fires occurring after fuels have cured in the fall or in the early spring before green-up may have been more significant than summer fires. High fuel moisture in July and August and concurrent slow rates of spread result in a smaller area being burned by an individual fire, compared to those fires occurring when fuels are cured in the fall (Steuter 1988). Given the highly variable fire regime in the past, burns of varying intensities at differing seasons are appropriate. Further, the interval between fires should be varied to best restore fire disturbance patterns of the Northern Great Plains. The strategy should avoid a uniformity in timing of burns or in intervals between burns that artificially simplifies what was probably a more complex system (Howe 1994).

SPECIAL HABITATS AND SENSITIVE SPECIES

Reinstituting a fire regime based on historical processes that includes burning at varying intervals and in differing seasons is the first step in developing a strategy for using fire to manage biological diversity on native rangelands in this region. The second step involves assessing the direct and indirect impacts of fire on special habitats and sensitive species. Special habitats are native biological communities or ecosystems that are rare, unique, or highly productive elements of regional landscapes (Salwasser 1990). Sensitive species include those native species currently in danger of extinction or those whose population trends are negatively affected by human actions (Salwasser 1990). The burning strategy should also consider the potentially different historical fire disturbance regimes in these sensitive ecosystems, minimize potential negative influences of fire, and maximize conditions favorable to the expansion of these systems and species.

The special habitats in the Northern Great Plains (wetlands, lowlands, and riparian areas) contain high numbers of listed vulnerable species (Finch 1992, Finch and Ruggiero 1993). Although each of these habitats constitutes a relatively small percentage of the total land area, each contributes disproportionately to the diversity of native rangelands in this region (Finch and Ruggiero 1993). If sensitive communities such as these occur within a management unit, burning programs should be examined relative to their impacts on these habitats. The range in frequency, timing, and intensity of burns suitable to upland habitats may not provide optimum conditions for sustaining these distinctive systems.

Wetlands, lowlands, and riparian woodlands in this region are examples of communities that, because of higher moisture, likely burned less frequently than uplands. Riparian zones throughout the region, and woody draws in the more arid portions, tend to be green throughout most of the growing season, have higher relative humidities than adjacent grasslands, and often have running water or moist soils that slow the spread of fire into these communities. In most years, prairie fires would skip over or only burn lightly through these narrow woodlands (Severson and Boldt 1978). However, the narrow configuration and close contact of these woodlands with flammable grassland fuels suggest that historically they were exposed to a high number of grassland fires. Fire inevitably entered these woodlands, especially in dry years on hot and windy days.

Given that the species composition in woody draws includes a number of deciduous species, such as snowberry and chokecherry, that sprout following burning (Wright and Bailey 1982), and that several woody species establish best in mineral soils, fire probably functioned as a regeneration mechanism in these systems. Further, since these communities stay green longer than uplands, fires probably burned late in the growing season when there were adequate levels of cured, fine fuel. Repeated, annual fires, especially during droughts, tend to favor the growth of grasses over woody plants (Wright and Bailey 1982). Fires occurring infrequently when plants dormant, followed by high precipitation, may enhance woody plant growth (Wright and Bailey 1982, Sieg 1991). If the goal is to regenerate woody plants in woody draws and/or to mimic historical fires, prescriptions should be set to achieve high intensities (Sieg 1996).

Rocky Mountain juniper woodlands are an example of a relatively uncommon community in the Western portion of the Northern Great Plains that rarely burned. In this region, Rocky Mountain juniper grows best on steep barren slopes (Noble 1990) where the sparse understory vegetation is rarely adequate to sustain a fire. In areas where fine fuels are sufficient to carry a fire, the high volatile oil content of the foliage combined with Rocky Mountain juniper's inability to sprout following topkilling, results in high mortality rates (Wright and Bailey 1982).

Threatened or endangered species are examples of sensitive species whose needs cannot be ignored. Because they are the first species to drop out of ecosystems, they are considered the weakest link in the conservation of native biological diversity (Finch and Ruggiero 1993). Providing habitats in an appropriate spatial and temporal arrangement is necessary to maintain viable populations of sensitive species. Thus, vegetation management is a major tool for maintaining and restoring biodiversity, and for delisting or avoiding listing of threatened and endangered species (Kaufmann et al. 1994).

Adjusting fire management programs to meet the needs of threatened and endangered species requires an understanding of the role of fire in the long-term sustainability of the ecosystems supporting these species, and in the life history and habitat needs of individual species. For example, the western prairie fringed orchid is a federally listed threatened plant species associated with swales (low-lying often wet land) of the tallgrass prairie (U.S. Fish and Wildlife Service 1989). Although the tallgrass prairie is prone to burn every 1 to 5 years (Collins and Gibson 1990), it is unlikely that swales supporting orchids burned as often, especially during years when they were flooded. Vogl(l969) describes a "quasi-equilibrium" of a Wisconsin lowland maintained by floods during wet periods and fires during droughts. Lowlands supporting orchid populations likely burned throughout the growing season during prolonged droughts; however, fires that occur when orchids are actively growing are apt to injure or kill them. Since fall burning allows orchids to complete their life cycle, and dry conditions and lightning are inclined to occur late in the growing season, fall fires are a better choice than spring burning to sustain orchid populations and their associated habitat (Bjugstad-Porter 1993).

MANAGE INTRODUCED SPECIES

The introduction of exotic species to new environments without their associated parasites and pests may be humankind's greatest environmental manipulation (Young and Evans 1976). Many invasive exotic species have characteristics that enable them to vigorously compete with native plants and to exploit disturbed areas (Parker et al. 1993). In addition to reviewing impacts of existing non-native species and preventing the introduction of new ones (Kaufmann et al. 1994), management plans should address how to manage these species; fire is a useful tool in this arena. Problem species include those purposely planted, such as smooth brome, and a variety of species accidentally introduced, such as cheatgrass, Japanese brome, and leafy spurge (Lym 1991).

Although burning is not a panacea for discouraging introduced species, with careful planning it can be a useful tool, especially if native species are not adversely affected. Burning at a time when plants are most vulnerable is useful for suppressing undesirable species. For example, burning in mid-or late May, when smooth brome tillers are either elongating or heading, reduces tiller density of smooth brome by 50 percent when compared to unburned plots in Nebraska (Willson 1992). Burning in May also enhances production of flowering culms of some native warm-season grasses such as big bluestem (Willson 1992). However, burning is not a cure-all for reducing persistent species such as smooth brome, and the outcome is strongly dependent on other factors such as climate and precipitation patterns. Subsequent burning in Pipestone, Minnesota failed to significantly reduce smooth tiller density (Willson and Stubbendieck 1996).

In addition to killing or injuring individual exotic plants, burning can be used to make the habitat less conducive to a species expansion. Spring burning in western South Dakota killed Japanese brome seedlings for one growing season, and by reducing litter accumulations, decreased future germination rates (Whisenant and Uresk 1990). In this case, spring burning was detrimental to the production of one native species, green needlegrass; enhanced production of two others, buffalo grass and sand dropseed; and did not change the production of a fourth, threadleaf sedge (Whisenant and Uresk 1990).

A combination of burning and other management tools may be valuable in managing invasive species. For example, picloram plus 2,4-D applied in the fall followed by spring burning reduced the stem density and germination rates of leafy spurge in North Dakota more than any other treatment tested (Wolters et al. 1994). The key to success in managing invasive species is to begin treatment before sive spread occurs and to focus as much as possible on the invaded ecosystem rather than on the invader (Hobbs and Humphries 1995).

SUMMARY

A strategy for using fire to manage native biological diversity on rangelands in the Northern Great Plains should consider natural disturbance patterns. Fires historically occurred as often as every 1 to 5 years in the more mesic portions of the region, but less frequently in areas of rough topography and in lowlands. Lightning, a major ignition source in this region, caused fires most often in July and August. American Indians accidentally or intentionally set fires in nearly every month of the year; however, the greatest number were set in April, September, and October. The end result of the erratic climate, fuels, topographic relief and factors such as grazing animals, was that the role of fire was not constant in time or space.

Reinstituting a fire regime based on historical processes, including burning at varying intervals (to reflect climatic patterns) and in differing seasons, is the first step in developing a strategy for using fire to manage for biological diversity on native rangelands in this region. Including mid-summer burns, rather than concentrating all prescribed burning in the spring and fall, would better mimic natural disturbance patterns. The second step involves adjusting fire regimes to best sustain special habitats, such as wetlands and riparian zones, and sensitive species, especially threatened and endangered ones. Third, fire prescriptions should be planned so that burning does not enhance the spread of invasive species. The overall goal is to base the fire management strategy on an understanding of historic processes and ecosystem interactions, and resist techniques that rely on unexamined conventions (Howe 1994).

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LITERATURE CITED

Anderson, Roger C. 1990. The historic role of fire in the North American grassland. In: Fire in North American Tallgrass Prairies. Collins, Scott L; Wallace, Linda L., eds. Norman, OK: Univ. Oklahoma Press. 8-18.

Bjugstad-Porter, Rochelle. 1993. The western prairie fringed orchid *(Platanthera praeclara):* it's response to burning and associated mycorrhizal fungi. Laramie, WY: University of Wyoming. 116 p. M.S. thesis.

Bragg, Thomas B. 1985. A preliminary fire history of the oak/pine forest of northcentral Nebraska. In: Proc. 95th Ann. Meet. Nebr. Acad. Sci., Lincoln, NE: Nebraska Wesleyan University. 8.

Bragg, Thomas B.; Hulbert, Lloyd C. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management. 29:19-24.

Brown, Peter M. and Carolyn Hull Sieg. 1996. Fire history in interior ponderosa pine communities of the Black Hills, South Dakota. International Journal fo Wildland Fire. 6:97-105.

Collins, Scott L. 1990. Introduction: fire as a natural disturbance in tallgrass prairie ecosystems. In: Fire in North American Tallgrass Prairies. Collins, Scott L; Wallace, Linda L., eds. Norman, OK: Univ. Oklahoma Press. 3-7.

Collins, Scott L.; Gibson, David J. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. In: Fire in North American Tallgrass Prairies. Collins, Scott L; Wallace, Linda L., eds. Norman, OK: Univ. Oklahoma Press. 81-98.

Finch, D.M. 1992. Threatened, endangered, and vulnerable species of terrestrial vertebrates in the Rocky Mountain Region. Gen. Tech. Rep. RM-215. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 38 pp.

Finch, Deborah M.; Ruggiero, Leonard F. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and Northern Great Plains. Natural Areas Journal. 13:191-203.

Fisher, R.F.; Jenkins, M.J.; Fischer, William F. 1987. Fire and the prairie-forest mosaic of Devils Tower National Monument. American Midland Naturalist 117:250-257.

Gehring, Janet L; Bragg, Thomas B. 1992. Changes in prairie vegetation under eastern red cedar (Juniperus *virginiana* L.) in an eastern Nebraska bluestem prairie. American Midland Naturalist

Great Plains Flora Association. 1986. Flora of the Great Plains. Lawrence, KS: Univ. Press of Kansas. 1392 pp.

Henderson, Richard A.; Statz, Sandra H. 1995. Bibliography of fire effects and related literature applicable to the ecosystems and species of Wisconsin. Technical Bulletin No. 187, Department of Natural Resources, Madison. 56 pp.

Higgins, Kenneth F. 1984. Lightning fires in North Dakota grasslands and in pine-savanna lands of South Dakota and Montana. Journal of Range Management. 37:100-103.

Higgins, Kenneth F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. Res. Pub. 161. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. 39 pp.

Hobbs, Richard J.; Humphries, Stella E. 1995. An integrated approach to the ecology and management of plant invasions. Conservation Biology. 9:761-770.

Howe, Henry F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology. 8:691-704.

Johnson, W. Carter; Burgess, Robert L.; Keammerer, Warren R. 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. Ecological Monograph. 46:59-84.

Kaufmann, Merrill R.; Graham, Russell T.; Boyce, Douglas A., Jr. [et al.]. 1994. An ecological basis for ecosystem management. Gen. Tech. Rep. RM-246. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 22 pp.

Lym, Rodney G. 1991. Economic impact, classification, distribution, and ecology of leafy spurge. In: Noxious Range Weeds. James, Lynn F.; Evans, John 0.; Ralphs, Michael H.; Child, R. Dennis, eds. Boulder, CO: Westview Press. 169-181.

Noble, Daniel L. 1990. *Juniperus scopulorum* Sarg. Rocky Mountain juniper. In: Silvics of North America, Vol. 1. Agric. Handb. 654. Burns, Russell M.; Honkala, Barbara H., Tech. Coords. Washington, DC: U.S. Department of Agriculture, Forest Service. 116-126.

Parker, Ingrid M.; Mertens, Shoshana K.; Schemske, Douglas W. 1993. Distribution of seven native and two exotic plants in a tallgrass prairie in southeastern Wisconsin: the importance of human disturbance. American Midland Naturalist. 130:43-55.

Risser, Paul G. 1990. Landscape processes and the vegetation of the North American grassland. In: Fire in North American Tallgrass Prairies. Collins, Scott L; Wallace, Linda L., eds. Norman, OK: Univ. Oklahoma Press. 133-146.

Risser, P.G.; Birney, E.C.; Blocker, H.D. [et al.]. 1981. The true prairie ecosystem. Stroudsburg, PA: Hutchinson Ross.

Salwasser, Hal. 1990. Conserving biological diversity: a perspective on scope and approaches. Forest Ecology and Management. 35:79-90.

Severson, Kieth E.; Boldt, Charles E. 1978. Cattle, wildlife, and riparian habitats in the western Dakotas. In: Management and use of Northern Plains rangeland Regional Rangeland Symposium; 1978 Feb. 27-28; Bismarck, ND: North Dakota State University. 91-103.

Sieg, Carolyn Hull. 1991. Ecology of bur oak woodlands in the foothills of the Black Hills, South Dakota. Lubbock, TX: Texas Tech University. 185 p. Ph.D. Thesis.

Sieg, Carolyn Hull. 1996. The role of prescribed burning in regenerating *Quercus macrocarpa* and associated woody plants in stringer woodlands in the Black Hills, South Dakota. International Journal of Wildland Fire. 6:21-29.

Steuter, A.A. 1988. Restoring a mixed prairie process: the fire-bison grazing interaction. Bulletin of the Ecological Society of America. 69:308.

Steuter, Allen A.; Grygiel, C.E.; Biondini, M.E. 1990. A synthesis approach to research and management planning: the conceptual development and implementation. Natural Areas Journal. 10:61-68.

U.S. Fish and Wildlife Service. 1989. Endangered and threatened wildlife and plants; determination of threatened status for *Platanthera leucophaea* (eastern prairie fringed orchid) and *Platanthera praeclara* (western prairie fringed orchid). Federal Register 54:39857-39862.

Vinton, Mary Ann; Hartnett, David C.; Finck, Elmer J.; Briggs, John M. 1993. Interactive effects of fire, bison (Bison *bison)* grazing and plant community composition in tallgrass prairie. American Midland Naturalist. 129:10-18.

Vogl, Richard J. 1969. One hundred and thirty years of plant succession in a southeastern Wisconsin lowland. Ecology. 50-248-255.

Wells, Philip V. 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains region. Science. 148:246-249.

Wendtland, Kyle J.; Dodd, Jerrold L. 1992. The fire history of Scotts Bluff National Monument. In: Proceedings of the 12th North American Prairie Conference; Smith, Daryl D.; Jacobs, Carol A., eds. 1990, August 5-9; Cedar Falls, IA: University of Northern Iowa. 141-143.

Whisenant, Steven G; Uresk, Daniel W. 1990. Spring burning Japanese brome in a western wheatgrass community. Journal of Range Management. 43:205-208.

Willson, Gary D. 1992. Morphological characteristics of smooth brome used to determine a prescribed burn date. In: Proceedings of the 12th North American Prairie Conference; Smith, Daryl D.; Jacobs, Carol A., eds. 1990, August 5-9; Cedar Falls, IA: University of Northern Iowa. 113-116.

Willson, Gary D.; Stubbendieck, James. 1996. Suppression of smooth brome by Atrazine, mowing and fire. The Prairie Naturalist.

Wolters, Gale L.; Sieg, Carolyn Hull; Bjugstad, Ardell J.; Gartner, F. Robert. 1994. Herbicide and fire effects on leafy spurge density and seed germination. Res. Note RM-526. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 5 pp.

Wright, Henry A.; Bailey, Arthur W. 1982. Fire Ecology. New York: John Wiley & Sons. 501 pp.

Young, James A.; Evans, Raymond A. 1976. Responses of weed populations to human manipulations of the natural environment. Weed Science. 24:186-190.

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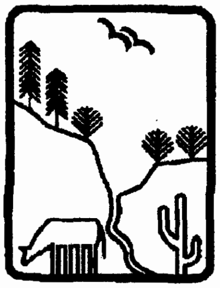

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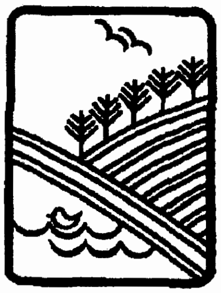

Great Plains

The Rocky Mountain Station is one of seven regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

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Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

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Research Article

Recreational Shooting of Prairie Dogs: A Portal for Lead Entering Wildlife Food Chains

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ABSTRACT Although lead shot has been banned for waterfowl hunting in North America, some predators continue to exhibit elevated lead burdens, which has been attributed to ingesting metallic lead from other projectiles. Few studies have investigated residual lead fragments in hunted upland animals. Therefore, specific portals for lead entering wildlife food chains remain largely unknown. Prairie dogs (*Cynomys* spp.) are shot for recreation with minimal regulation in western North America. Because recreational shooters mostly use expanding bullets and rarely remove or bury carcasses, shot prairie dogs could make lead accessible to predators and scavengers. To determine whether and to what degree shot prairie dogs carry lead fragments, we analyzed carcasses shot by recreational shooters with 2 bullet types. Bullet type influenced the probability of bullet fragments being retained in carcasses; 87% of prairie dogs shot with expanding bullets contained bullet fragments, whereas 7% of carcasses shot with non-expanding bullets did. The amount of bullet fragments per carcass also differed between bullet types; carcasses shot with expanding bullets contained a mean of 228.4 mg of the lead-containing bullet core and 74.4 mg of the copper-alloy jacket, whereas carcasses shot with non-expanding bullets averaged only 19.8 mg of the core and 23.2 mg of the jacket. Lead fragments in carcasses shot with expanding bullets were small in size; 73% of all lead mass in each carcass was from fragments that weighed <25 mg each, small enough to be easily ingested and absorbed by secondary consumers. The amount of lead in a single prairie dog carcass shot with an expanding bullet is potentially sufficient to acutely poison scavengers or predators. Therefore, shot prairie dogs may provide an important portal for lead entering wildlife food chains and may pose risks to raptors and carnivores. Managers should consider measures, such as using non-expanding or lead-free ammunition, to reduce the likelihood of lead consumption and poisoning in upland wildlife. (JOURNAL OF WILDLIFE MANAGEMENT 71(1):103–108; 2007)

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The potential of ingested elemental lead to kill or sicken free-ranging vertebrates, particularly birds, is well documented. Lead is not physiologically valuable to vertebrates at any dose or concentration (Pain 1995). Waterfowl (Grinnell 1894, Wetmore 1919), upland game birds (Calvert 1876), and raptors (Locke et al. 1969, Jacobson et al. 1977) have been shown to ingest lead from various human sources (Pain 1995), particularly spent shotgun pellets (Kendall et al. 1996). Following documentation of widespread lead shot ingestion and poisoning in waterfowl and their predators, the use of lead shot for waterfowl hunting was banned in the United States in 1991 (Anderson 1992) and Canada in 1997 (Clark and Scheuhammer 2003). However, these bans have not eliminated lead exposure in wildlife; lead levels in eagles remain elevated (Kramer and Redig 1997). Further, raptors not typically associated with aquatic food chains are poisoned from ingesting lead: rough-legged hawks (*Buteo lagopus*; Craig et al. 1990), prairie falcons (*Falco mexicanus*; Benson et al. 1974), red-tailed hawks (*Buteo jamaicensis*; Sikarskie 1977), golden eagles (*Aquila chrysaetos*; Wayland et al. 2003), and California condors (*Gymnogyps californianus*; Janssen et al. 1986). Lead poisoning among raptors appears to come primarily from ingestion of metallic lead from ammunition used in hunting (Clark and Scheuhammer 2003). Secondary intoxication appears not to be important; tissues from animals that have ingested lead shot contain insufficient lead to cause symptoms in predators that consume them (Redig et al. 1980, Pattee and Hennes 1983). Thus, continued lead poisoning among carnivores and raptors appears to result mostly from ingestion of lead fragments in hunted vertebrate carcasses.

Over much of their temperate grassland range, prairie dogs (*Cynomys* spp.), colonial sciurids of North America, are subjected to unregulated human shooting (Pauli 2005). Not hunted for meat or skin, prairie dogs are used as targets by recreational shooters typically employing high-velocity rifles effective at ≤500 m. With such a weapon, and lacking state or federal regulations limiting animal harvest, a single shooter may kill scores of prairie dogs from one colony in a single session (>170 prairie dogs in one instance [Vosburgh and Irby 1998]). In recent years, recreational shooters have reported killing >2 million black-tailed prairie dogs (*Cynomys ludovicianus*) per year from 3 states combined (Reeve and Vosburgh 2005). Because shooters typically do not retrieve or bury shot prairie dogs, the carcasses are available to predators and scavengers. Unpublished accounts suggest that rates of removal, and presumably ingestion, of these carcasses by scavengers are high. Typically, recreational shooters use expanding bullets, which fragment on impact (Nunamaker and Berg 1985). Therefore, recreational shooting of prairie dogs may present a widespread source of lead to raptors and carnivores within the geographic range of prairie dogs.

To better understand the potential of shot prairie dogs to be a portal for lead entering wildlife food chains, we conducted detailed analyses of carcasses of prairie dogs that had been shot by recreational shooters. Our objectives were 3-fold: 1) to determine whether recreationally shot prairie dog carcasses contained substantive amounts of lead; 2) to assess whether the bullet type (expanding vs. non-expand-

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ing) used by shooters influenced the retention of bullet parts in the carcass; and 3) to quantify the number, size, and mass of bullet fragments in prairie dog carcasses and the surface area of lead exposed to the gut of a consumer of these carcasses.

STUDY AREA

We conducted this study while investigating the population biology of black-tailed prairie dogs around Thunder Basin National Grassland (105°13′N, 43°42′W), Wyoming, USA, in summers 2003–2004. Thunder Basin National Grassland encompassed >230,000 ha of federal land within a mixture of public and private lands in northeastern Wyoming. The region was characterized by mixed-grass prairie and sagebrush steppe habitat. Because of the large number of black-tailed prairie dog colonies in the region, Thunder Basin National Grassland was subjected to intense recreational shooting.

METHODS

Field Methods

Black-tailed prairie dogs were shot opportunistically with a .223 caliber rifle (M77; Sturm, Ruger and Co., Inc., Southport, CT) by volunteer shooters at 3 colonies located on private land. To determine whether the type of bullet influenced lead burdens in carcasses, we used 2 different bullet types: 1) 55-grain (nominal) non-expanding full metal jacketed bullets (Eldorado Cartridge Corp., Boulder City, NV), in which the bullet core, except for its base, is encased in a copper jacket; and 2) 55-grain (nominal) expanding soft-pointed bullets (Black Hills Ammunition, Rapid City, SD), in which the tip of the lead bullet core is exposed. To mimic typical shooting events, we shot prairie dogs at distances of 20–200 m. After each shooting session, we collected and froze carcasses until we processed them in the laboratory.

Laboratory Methods

We radiographed each animal laterally and then scanned radiographs into the computer program ImageJ (Rasband 2004), which counted the number of bullet fragments in each carcass and measured the projected surface area of each fragment from the radiograph. Because we were unable to distinguish material from the bullet core (about 98% lead, 2% antimony) from the bullet jacket (about 90% copper, 10% zinc) in radiographs and digitized images, we extracted all bullet fragments from a random sample of 10 carcasses shot with expanding bullets that retained bullet fragments. Only 2 carcasses shot with non-expanding bullets contained visible metallic fragments; we extracted fragments from both of them.

To extract bullet fragments, we boiled each carcass in a pressure cooker for 6–8 hours. We poured off the supernatant and added 35.0 g of protease bleach to dissolve remaining soft tissue, which we diluted with 3.5 L of purified water and let digest at 20° C for 48 hours. We again discarded the supernatant and removed and inspected all bones for bullet fragments. We extracted large bullet fragments manually, identified them as either core or jacket, and weighed them to the nearest 0.1 mg on a digital balance. We collectively rinsed small, unidentifiable particles (<1 mg) and set them aside for quantitative analysis. We used flame atomic absorption spectrometry (AAS) to estimate the mass of lead and copper, and we used inductively coupled plasma mass spectrometry (ICP-MS) to estimate the amount of secondary elements, antimony and zinc, in the unidentifiable fragments.

We prepared samples for AAS and ICP-MS using standard procedures (Schmitt et al. 1988, Krueger and Duguay 1989, Tam and Yao 1999). Briefly, we dissolved each sample in 10 mL of HNO_3 and heated each in a water bath (65° C) for 24 hours. We centrifuged samples and diluted the supernatant with 50 ml of ultrapure water. We diluted a 0.5-mL aliquot to 10 mL with ultrapure water. We analyzed diluted samples with AAS for copper and lead and with ICP-MS for zinc and antimony, again following standard procedures. For quality assurance, we employed one blank of diluted HNO_3 and one control, which was from a prairie dog carcass that did not contain any bullet fragments but went through the entire extraction process.

For each of the 12 carcasses, we estimated core and jacket masses by combining the mass estimate of lead from AAS with the mass estimate of antimony from ICP-MS and similarly combining the mass estimates of copper with those of zinc. To estimate the total amount of core and jacket material in each carcass, we combined the masses of large fragments of core and jacket to those of small fragments estimated from ICP-MS and AAS. These values were compared with those for unfired bullets, which we also separated into jacket and core and weighed on a digital balance.

Statistical Analyses

We compared the proportion of carcasses with bullet fragments between expanding and non-expanding bullets with the Fisher exact test. For carcasses shot with expanding bullets for which we measured radiographic attributes and extracted mass of the bullet core and jacket ($n = 10$), we fitted a series of simple linear regression models predicting the mass of core material, jacket material, and total bullet material from 2 predictor variables: 1) the number of bullet fragments in the radiograph and 2) the total projected surface area of the fragments in the radiograph. We employed each predictor variable separately because predictor variables were highly collinear (all $r^2 > 0.95$) and combining them for multiple linear regression analyses did not improve the overall predictive power of the models. We simplified all models by forcing the regression through the origin (no surface area or particles equated with zero mass). We selected the models with the highest correlation coefficients and predicted the mass of core material, jacket material, and total bullet material for carcasses shot with expanding bullets from which we did not extract bullet fragments.

We combined estimates for the amount of core, jacket, and total bullet material in prairie dogs shot with expanding bullets using a weighted mean ($\bar{x}_w$) because variances associated with these measured (weighed) and predicted values differed. We calculated the weighted mean for each bullet fragment type with the equation $\bar{x}_w = w_m\bar{x}_m + w_p\bar{x}_p$, where w_m and w_p are the weighting factors applied to the measured ($\bar{x}_m$) and predicted ($\bar{x}_p$) mean mass of core, jacket, and total bullet material. We calculated weighting factors (Neter et al. 1990, Lipsey and Wilson 2001) from the variances of measured (V_m) and predicted (V_p) values using the following equations:

$$w_m = \frac{\frac{1}{V_m}}{\frac{1}{V_m} + \frac{1}{V_p}} \text{ and } w_p = \frac{\frac{1}{V_p}}{\frac{1}{V_m} + \frac{1}{V_p}}.$$

Similarly, we generated a combined standard deviation for the mass of metals from measured and predicted samples as $SD(\bar{x}_w) = \sqrt{w_m^2 V_m + w_p^2 V_p}$.

RESULTS

Radiographs revealed that the presence–absence of bullet fragments in carcasses differed between bullet types ($P <$ 0.0001, Fisher exact test); only 2 of 29 (7%) prairie dogs shot with non-expanding bullets contained bullet fragments, whereas the majority, 26 of 30 (87%), of prairie dogs shot with expanding bullets held fragments (see Fig. 1 for example). The 2 carcasses with fragments of non-expanding bullet each contained a small amount of both components, averaging 19.8 mg of core material (98% of which was lead) and 23.2 mg of jacket material, or approximately 1.2% ($\bar{x}_m$ = 43.0 mg) of the original mass of the bullet (Table 1).

All 10 randomly selected carcasses with expanding bullet fragments contained core and jacket material in much larger quantities; carcasses averaged 235.7 mg of core material (98% of which was lead) and 82.1 mg of jacket material (Table 1). In total, carcasses retained 317.8 mg of bullet fragments, 9.0% of the original expanding bullet. The individual fragments of core material in carcasses shot with expanding bullets were predominantly small; 73.1 ± 9.3% of all core material was from fragments that weighed <25 mg each (Fig. 2). Metal concentrations in our blank and control were below detection thresholds.

Regression models developed from carcasses for which bullet mass was measured exhibited a strong relationship between attributes in the radiographs and mass of fragments in the carcasses (Fig. 3; t-tests for all slope parameters had df = 10, $t > 6.0$, and $P < 0.005$). The total surface area of fragments in radiographs was the best predictor of the mass of core material (Fig. 3a), whereas the number of fragments in radiographs was the best predictor of the mass of jacket material (Fig. 3b) and total bullet material (Fig. 3c). The averages of predicted values from the regression equations ($\bar{x}_p$) were similar to those directly measured: 225.1 mg of core material, 73.5 mg of jacket material, and 256.2 mg of total bullet material.

Combining the measured values with predicted values in a weighted mean ($\bar{x}_w$) revealed that 8.3% (228.4 mg) of the core, 9.1% (74.4 mg) of the jacket, and 7.5% (265.4 mg) of the total bullet remained behind in prairie dogs shot with expanding bullets (Table 1). There was, however, high variation in the amount of bullet core in those carcasses (range: 5.1–774.5 mg). Nevertheless, considering only carcasses that contained fragments, prairie dogs shot with expanding bullets averaged >11 times more bullet core than those shot with non-expanding bullets (228.4 mg/19.8 mg; Table 1).

Figure 1. Lateral radiograph of a black-tailed prairie dog carcass (no. 1688) shot with an expanding bullet from a .223 caliber rifle, Thunder Basin, Wyoming, USA, 2004. Bullet fragments (white) are distributed through much of the carcass. In this carcass, 28.3% (774.5 mg) of the bullet core and 55.0% (449.1 mg) of the jacket was retained. We show a United States penny (diameter = 1.90 cm) for scale.

Considering all carcasses shot with non-expanding bullets, including those containing no detectable bullet fragments, carcasses retained about 0.1% (1.4 mg) of the core, 0.2% (1.6 mg) of the jacket, and 0.1% (3.0 mg) of the total bullet (Table 2). By contrast, the recomputed weighted mean ($\bar{x}_w$), incorporating the 4 of 30 carcasses of animals shot with expanding bullets that did not contain detectable bullet fragments, revealed that 7.5% (206.0 mg) of the core, 8.8%

Table 1. Mean mass and standard deviation of bullet components (jacket, core, and total bullet) recovered from and predicted to be in black-tailed prairie dog carcasses shot with non-expanding and expanding bullets, Thunder Basin, Wyoming, USA, 2004. We provide the mean mass of each component for unfired bullets, bullet fragments measured directly from shot prairie dogs, bullet fragments predicted from a regression equation, and the combined mean. We show values only for carcasses that contained detectable bullet fragments (2 of 29 for non-expanding bullets and 26 of 30 for expanding bullets).

	Non-expanding bullet (mg)							Expanding bullet (mg)						
		Jacket		Core		Total bullet			Jacket		Core		Total bullet	
	n	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	*n*	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Unfired	5	1,059.4	14.5	2,494.6	2.7	3,554.0	15.4	5.0	816.0	3.0	2,742.4	3.2	3,558.4	4.0
Measured[a]														
>1 mg	2	23.2	8.9	19.8	20.2	43.0	29.1	10.0	80.8	136.3	149.8	179.1	230.7	229.0
<1 mg	2	0.0	0.0	0.0	0.0	0.0	0.0	10.0	1.2	2.6	85.9	107.3	87.1	109.9
Total	2	23.2	8.9	19.8	20.2	43.0	29.1	10.0	82.1	138.1	235.7	281.2	317.8	383.1
Predicted	0	—[b]	—	—	—	—	—	16.0	73.5	45.9	225.1	187.5	256.2	160.1
Combined[c]	0	—	—	—	—	—	—	26.0	74.4	43.6	228.4	156.0	265.4	147.7

[a] We weighed fragments >1 mg on a digital balance; we estimated fragments <1 mg using spectrometry.

[b] Dash indicates value is incalculable.

[c] We combined measured and predicted means with a weighted equation.

(71.6 mg) of the jacket, and 7.1% (251.0 mg) of the total bullet were retained (Table 2).

DISCUSSION

Depending on bullet type, prairie dogs shot by recreational shooters contained variable but potentially substantive amounts of metallic lead. Of carcasses shot with expanding bullets, 87% contained detectable metallic lead, whereas only 7% carcasses shot with non-expanding bullets did. The carcasses shot with expanding bullets that contained bullet fragments detectable with radiography held large quantities of lead. Non-expanding bullets, by contrast, tended to pass through prairie dogs, leaving small or undetectable amounts of lead. This lead likely originated from the unjacketed base of the non-expanding bullets. In all, considering the bullet-

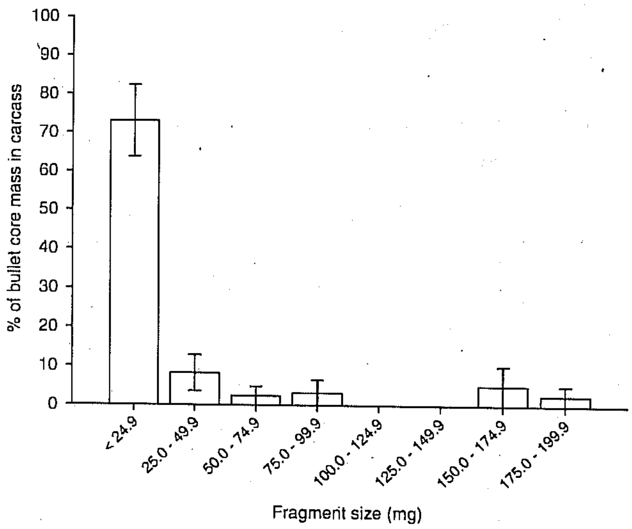

Figure 2. Histogram depicting the relative amount of different-sized bullet core fragments in prairie dogs shot with expanding bullets from a .223 caliber rifle (±1 SD), Thunder Basin, Wyoming, USA, 2004. The majority, 73.1%, of all bullet core fragments in carcasses were from the smallest fragment size, with each fragment weighing <24.9 mg.

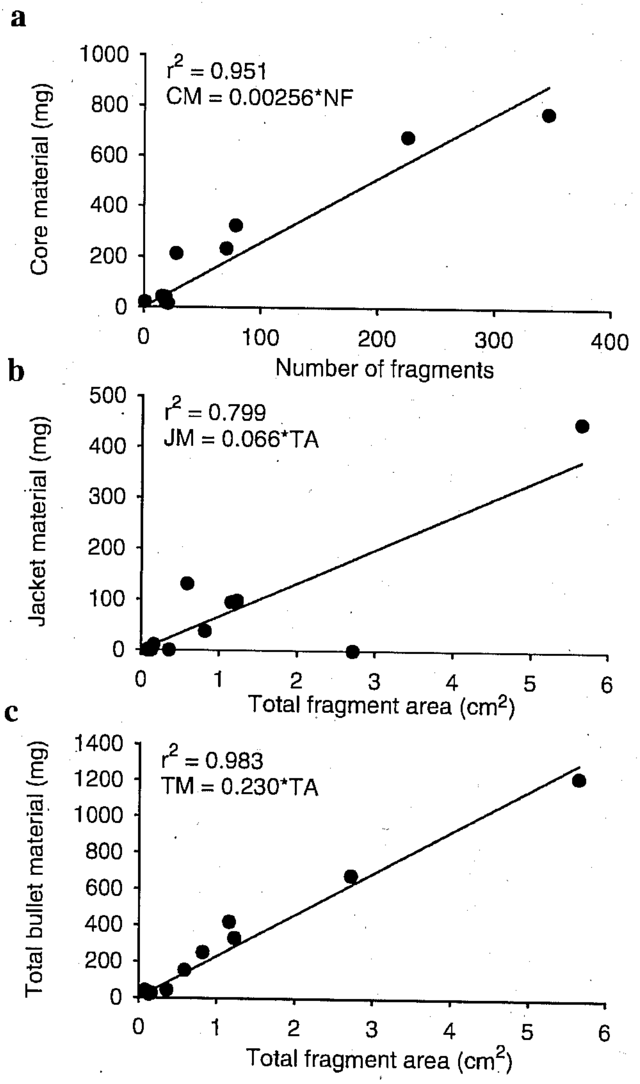

Figure 3. Regression models predicting the mass of (a) core material (CM), (b) jacket material (JM), and (c) total bullet material (TM) in prairie dog carcasses shot with .223 caliber expanding bullets from the number of bullet fragments (NF) and total surface area (TA) of bullet fragments in the radiographs of the carcasses, Thunder Basin, Wyoming, USA, 2004. We used these models to predict the mass of each bullet component for carcasses from which we had not extracted fragments.

Table 2. Mean mass and standard deviation of bullet components (jacket, core, and total bullet) for all prairie dog carcasses shot with non-expanding and expanding bullets, including those that contained no bullet fragments, Thunder Basin, Wyoming, USA, 2004.

		Jacket (mg)		Core (mg)		Total bullet (mg)	
Bullet type	***n***	$\bar{x}$	**SD**	$\bar{x}$	**SD**	$\bar{x}$	**SD**
Non-expanding	29	1.6	6.2	1.4	6.4	3.0	12.4
Expanding	30	71.6	44.1	206.0	150.2	251.0	149.3

type differences in presence of fragments in carcasses, the expanding bullets used in our study left nearly 150 times as much metallic lead in prairie dog carcasses as did non-expanding bullets. Further, bullet fragments in carcasses shot with expanding bullets were mostly very small; >70% of the retained bullet core mass, 98% of it lead, was in particles <25 mg in weight. This small fragment size increases the surface area of metallic lead and its uptake in animals that consume the fragments, relative to larger particles, such as typical shotgun pellets (Barltrop and Meek 1979).

Prairie dogs are commonly preyed upon or scavenged by many birds and mammals. At least 10 species of mammals and 9 species of raptors, including the black-footed ferret (*Mustela nigripes*) and bald eagle (*Haliaeetus leucocephalus*), have been reported predating or scavenging prairie dogs (Hillman 1968, Hoogland 2003). Raptors in particular are susceptible to lead poisoning; as little as 180 mg of metallic lead powder can kill nestling raptors (Hoffman et al. 1985) and only 2 g of lead shot is sufficient to kill adult eagles (Pattee et al. 1981). We found that 47% of prairie dogs shot with expanding bullets contained >180 mg of elemental lead, enough to be acutely lethal to nestling raptors and, depending on the absorption rate of the bullet fragments, an amount potentially sufficient to be acutely lethal to adult raptors as well. Of course, for both birds and mammals, a wide range of sublethal toxic effects are also possible from smaller quantities of lead, which could alter population processes such as survival and reproduction (Pain 1995).

In general, pellets from shotgun ammunition are large enough for scavengers to detect and avoid while feeding (Stendell 1980) and when incidentally ingested, raptors often regurgitate pellets before being completely digested (Platt 1976, Pattee et al. 1981). These mechanisms may reduce ingestion and assimilation of lead shot in prey or carrion. However, we found that >70% of lead was in fragment sizes likely too small (<25 mg) to be avoided during ingestion and perhaps too small to be egested through regurgitation of indigestible material. These small bullet core fragments each weighed <25 mg, which is about 0.1× the size of a no. 4 lead pellet. Small lead fragments are readily absorbed in the gastrointestinal tract (Barltrop and Meek 1979). Therefore, recreational shooting using expanding lead alloy bullets may present a particularly important portal for the entry of lead into wildlife food chains.

MANAGEMENT IMPLICATIONS

Our results suggest that recreational shooting of prairie dogs contributes to the problem of lead intoxication in wildlife food chains that include prairie dogs. Indeed, some features of recreational shooting, including the killing of large numbers of animals, not removing carcasses from the field, and using expanding bullets, is in contrast to traditional forms of hunting and may present potentially dangerous amounts and particle sizes of metallic lead to scavengers and predators of prairie dogs. Recreational shooting of black-tailed prairie dogs occurs with minimal regulation, yet appears to provide a readily available source of lead to scavenging vertebrates. Few agencies regulate recreational shooting intensity and duration, and none currently regulate the type of ammunition that can be used. Managers should consider measures, such as using non-expanding or lead-free ammunition, to reduce the likelihood of lead poisoning in scavenging raptors and carnivores.

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LITERATURE CITED

Anderson, W. L. 1992. Legislation and lawsuits in the United States and their effects in nontoxic shot regulations. Pages 56–60 *in* D. J. Pain, editor. Lead poisoning in waterfowl. International Waterfowl and Wetlands Research Bureau Special Publication 15, Slimbridge, United Kingdom.

Barltrop, D., and F. Meek. 1979. Effect of particle size on lead absorption from the gut. Archives of Environmental Health 34:280–285.

Benson, W. W., B. Pharaoh, and P. Miller. 1974. Lead poisoning in a bird of prey. Bulletin of Environmental Contamination and Toxicology 11: 105–108.

Calvert, H. J. 1876. Pheasants poisoned by swallowing shots. Field 47:189.

Clark, A. J., and A. M. Scheuhammer. 2003. Lead poisoning in upland-foraging birds of prey in Canada. Ecotoxicology 12:23–30.

Craig, T. H., J. W. Connelly, E. H. Craig, and T. L. Parker. 1990. Lead concentrations in golden and bald eagles. Wilson Bulletin 102:130–133.

Grinnell, G. 1894. Lead-poisoned ducks. Field and Stream 42:117–118.

Hillman, C. N. 1968. Field observations of black-footed ferrets in South Dakota. Transactions of the North American Wildlife and Natural Resources Conference 33:433–443.

Hoffman, D. J., J. C. Franson, O. H. Pattee, C. M. Bunck, and A. Anderson. 1985. Survival, growth, and accumulation of ingested lead in nestling American kestrels (*Falco sparverius*). Archives of Environmental Contamination and Toxicology 14:89–94.

Hoogland, J. L. 2003. Black-tailed prairie dog *Cynomys ludovicianus* and allies. Pages 232–247 *in* G. A. Feldhammer, B. C. Thompson, and J. A.

Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Jacobson, E., J. W. Carpenter, and M. Novilla. 1977. Suspected lead toxicosis in a bald eagle. Journal of the American Veterinary Medical Association 171:952–954.

Janssen, D. L., J. E. Oosterhuis, J. L. Allen, M. P. Anderson, D. G. Kelts, and S. N. Wiemeyer. 1986. Lead poisoning in free-ranging California condors. Journal of the American Veterinary Medical Association 189: 1115–1117.

Kendall, R. J., T. E. Lacher, Jr., C. Bunck, B. Daniel, C. Driver, C. E. Grue, F. Leighton, W. Stansley, P. G. Watanabe, and M. Whithworth. 1996. An ecological assessment of lead shot exposure in non-waterfowl avian species: upland game birds and raptors. Environmental Toxicology and Chemistry 15:4–20.

Kramer, J. L., and P. T. Redig. 1997. Sixteen years of lead poisoning in eagles, 1980–1995: an epizootiologic view. Journal of Raptor Research 31:327–332.

Krueger, J. A., and K. M. Duguay. 1989. Comparative analysis of lead in Maine urban soils. Bulletin of Environmental Contamination and Toxicology 42:574–581.

Lipsey, M. W., and D. B. Wilson. 2001. Practical meta-analysis. Sage, Thousand Oaks, California, USA.

Locke, L. N., G. E. Bagley, D. N. Frickie, and L. T. Young. 1969. Lead poisoning and aspergillosis in an Andean condor. Journal of the American Veterinary Medical Association 155:1052–1056.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs. Third edition. Richard D. Irwin, Homewood, Illinois, USA.

Nunamaker, D. M., and P. Berg. 1985. Open fractures and gunshot injuries. Pages 481–497 *in* C. D. Newton and D. M. Nunamaker, editors. Textbook of small animal orthopaedics. J. B. Lippincott, Philadelphia, Pennsylvania, USA.

Pain, D. J. 1995. Lead in the environment. Pages 356–391 *in* D. J. Hoffman, B. A. Rattner, G. A. Burton, Jr., and J. Cairns, Jr., editors. Handbook of ecotoxicology. Lewis Publishers, Boca Raton, Florida, USA.

Pattee, O. H., and S. K. Hennes. 1983. Bald eagles and waterfowl: the lead shot connection. Transactions of the North American Wildlife and Natural Resource Conference 48:230–237.

Pattee, O. H., S. N. Wiemeyer, B. M. Mulhern, L. Sileo, and J. W. Carpenter. 1981. Experimental lead-shot poisoning in bald eagles. Journal of Wildlife Management 45:806–810.

Pauli, J. N. 2005. Ecological studies of the black-tailed prairie dog (*Cynomys ludovicianus*): implications for biology and conservation. Thesis, University of Wyoming, Laramie, USA.

Platt, J. B. 1976. Bald eagles wintering in a Utah desert. American Birds 30: 783–788.

Rasband, W. S. 2004. ImageJ. National Institutes of Health, Bethesda, Maryland, USA. <http://rsb.info.nih.gov/ij/.> Accessed 5 Apr 2005.

Redig, P. T., C. M. Stowe, D. M. Barnes, and T. D. Arent. 1980. Lead toxicosis in raptors. Journal of the American Veterinary Medical Association 177:941–942.

Reeve, A. F., and T. C. Vosburgh. 2005. Recreational shooting of prairie dogs. Pages 139–156 *in* J. L. Hoogland, editor. Conservation of the black-tailed prairie dog. Island Press, Washington, D.C., USA.

Schmitt, M. D. C., D. J. Trippler, J. N. Wachtler, and G. V. Lund. 1988. Soil lead concentrations in residential Minnesota as measured by ICP-AES. Water, Air, and Soil Pollution 39:157–168.

Sikarskie, J. 1977. The case of the red-tailed hawk. Intervet 8:4.

Stendell, R. C. 1980. Dietary exposure of kestrels to lead. Journal of Wildlife Management 44:527–530.

Tam, N. F. Y., and M. W. Y. Yao. 1999. Three digestion methods to determine concentrations of Cu, Zn, Cd, Ni, Pb, Cr, Mn, and Fe in mangrove sediments from Sai Keng, Chek Keng, and Sha Tau Kok, Hong Kong. Bulletin of Environmental Contamination and Toxicology 62:708–716.

Vosburgh, T. C., and L. R. Irby. 1998. Effects of recreational shooting on prairie dog colonies. Journal of Wildlife Management 62:363–372.

Wayland, M., L. K. Wilson, J. E. Elliott, M. J. R. Miller, T. Bollinger, M. McAdie, K. Langlier, J. Keating, and J. M. W. Frose. 2003. Mortality, morbidity and lead poisoning of eagles in western Canada, 1986–1998. Journal of Raptor Research 37:8–18.

Wetmore, A. 1919. Lead poisoning in waterfowl. U.S. Department of Agriculture Bulletin 793:1–12.

Associate Editor: Mills.

Toxicity reference values for chlorophacinone and their application for assessing anticoagulant rodenticide risk to raptors

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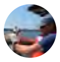

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United States Geological Survey
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United States Geological Survey
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Department of Pesticide Regulation

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M E M O R A N D U M

TO: Ann Prichard, Chief
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DATE: June 27, 2013

SUBJECT: SECOND GENERATION ANTICOAGULANT RODENTICIDE ASSESSMENT

In a July 2011 memorandum, the California Department of Fish and Game (CDFG) requested that the Department of Pesticide Regulation (DPR) designate all second generation anticoagulant rodenticides as California restricted materials. This paper represents DPR's assessment, based on available data, of the potential and actual risk to non-target wildlife from second generation rodenticides.

Executive Summary

Commensal mice and rats pose a significant economic and health risk to people. The rodenticides that are utilized to control them need to be efficacious while being relatively safe for humans, pets, and non-target wildlife. Rodenticides currently registered for use in California fall into three categories: first generation anticoagulant rodenticides (chlorophacinone, diphacinone and warfarin), second generation anticoagulant rodenticides (brodifacoum, bromadiolone, difenacoum, and difethialone), and non-anticoagulant rodenticides (bromethalin, cholecalciferol, and zinc phosphide).

Compared to first generation rodenticides, second generation anticoagulant rodenticides are considered to be more effective as they only require a single feeding and no resistance has been reported. Based on animal LD_{50}s, second generation anticoagulant rodenticides have significantly longer half-lives in target and non-target wildlife, and are more toxic to birds and mammals.

DPR analyzed wildlife incident and mortality data between 1995 and 2011, and rodenticide use and sales data between 2006 and 2010. The data indicate that exposure and toxicity to non-target wildlife from second generation anticoagulant rodenticides is a statewide problem. In addition, the data suggest that the problem exists in both urban and rural areas. Research data from various locations throughout California indicate that exposure is occurring in many taxa and in various ecosystems (urban, suburban, rural, and natural/wild areas). While the data show exposure, they do not link specific uses, or location of use of second generation anticoagulant rodenticide (i.e., indoors or outdoors, homeowners or professionals) to exposure.

Of the 492 animals analyzed between 1995 and 2011, approximately 73% had residues of at least one second generation anticoagulant rodenticide. Brodifacoum residues were found in approximately 69% of the 492 animals, and brodifacoum was likely involved in 13% of animal mortalities. Bromadiolone residues were found in approximately 37% of the animals analyzed, and bromadiolone was likely involved in approximately 3% of animal mortalities. Difethialone residues were found in approximately 8% of the animals analyzed. Due to its relatively new entrance into the marketplace, animals were not analyzed for difenacoum residues. While no animal mortalities can be directly attributed to difethialone or difenacoum, based on half-life and toxicity data, these two chemicals appear to be similar to brodifacoum and bromadiolone. Animals that tested positive for second generation rodenticides include bobcats, mountain lions, coyotes, foxes, skunks, hawks, crows, and owls.

The data also show that exposure of wildlife to second generation anticoagulant rodenticides can lead to sub-lethal effects. The sub-lethal effects reduce the fitness of wildlife at a time when wildlife are already meeting numerous challenges. Riley et al's (2007) study of bobcats is an example of the sub-lethal effects of rodenticides. The bobcats died due notoedric mange. Mange was not previously known as a significant pathogen in wild felids. However, exposure to rodenticides appears to have contributed to the disease process, and hence, the mortality of the bobcats.

Based on the data reviewed, DPR finds that the use of second generation rodenticides presents a hazard related to persistent residues in target animals resulting in impacts to non-target wildlife.

Background

Commensal mice and rats pose a significant economic and health risk to people, as they can damage homes, destroy crops, contaminate food, and directly spread eleven diseases (Center for Disease Control (CDC, 2011(b)) and indirectly spread fifteen diseases (CDC, 2012(a)) that threaten people's health and lives. Therefore, controlling them is considered a priority.

Rodenticides are pesticides that are designed to kill rodents, including mice and rats. For the purposes of this document, rodenticides will be divided into anticoagulant rodenticides (first and second generation) and non-anticoagulant rodenticides (including bromethalin, cholecalciferol, and zinc phosphide). Strychnine will not be discussed as its only labeled use is for below-ground gopher control.

First generation anticoagulant rodenticides - chlorophacinone, diphacinone, and warfarin - were developed and marketed beginning in 1950. However, by the 1970's, resistance to warfarin was noted in Norway rats, roof rats, and mice in Europe and North America. The warfarin-resistant strains of mice and rats prompted the development of second generation anticoagulant rodenticides, including brodifacoum, bromadiolone, difethialone, and difenacoum. Brodifacoum was developed in 1975, registered with the United States Environmental Protection Agency (U.S. EPA) in 1979, and registered with DPR in 1983. DPR first registered bromadiolone in 1982. The remaining two second generation rodenticides are relatively new. DPR first registered difethialone in 1997 and difenacoum in 2008.

Both first and second generation anticoagulant rodenticides are vitamin K antagonists that cause mortality by blocking an animal’s ability to produce several key blood clotting factors. The result is a lag time between ingestion and death. The chemicals are likely to be additive in their effect (Gabriel et al (2012) and Riley et al (2007)), and can be treated with vitamin K (Merck Sharp & Dohme Corp (2011)). However, they differ in several key ways. First generation anticoagulant rodenticides require consecutive days of intake to accumulate a lethal dose and if the animal survives or doesn’t like the taste or effects, it may develop bait shyness. If an animal consumes an anticoagulant rodenticide is eaten by a predator, the predator can become affected by the rodenticide (Townsend et al, 1984). However, the ability of first generation rodenticides to bioaccumulate in target and non-target animals is considered low (Eason and Ogilvie, 2009). The half-life (the amount of time it takes a substance to reduce its concentration by half) of most first generation anticoagulants in both target and non-target wildlife is generally hours to days, compared to the half-lives of second generation anticoagulants which are generally days to months. See Table 1 (below).

Second generation anticoagulant rodenticides have the same mechanism of action, but they have a higher affinity for the target enzyme (epoxide reductase enzyme), the ability to disrupt the vitamin K(1)-epoxide cycle at more points, and significantly longer half-lives in blood and liver (Watt et al, 2005) than first generation anticoagulant rodenticides. In general, rodents require only one feeding of bait to receive a lethal dose, although bromadiolone and difenacoum may require multiple feedings. Because it takes several days for the rodent to die, animals often eat multiple doses, allowing for super-lethal concentrations of the rodenticide to accumulate in its body. Second generation anticoagulant rodenticides become established in the animal’s liver, with liver half-lives of four months to a year. If an animal that consumes a second generation anticoagulant rodenticide is eaten by a predator, the predator can become affected by the rodenticide. Because of their long half-lives, these rodenticides bioaccumulate in non-target wildlife (Annex I- Norway, 2007). See Table 1 (below).

The three non-anticoagulant rodenticides belong to three different chemical classes and differ from each other in their modes of action. Bromethalin is a neurotoxin that causes increased intracranial pressure and depending upon the dose, vomiting, seizures, paralysis, and death. Cholecalciferol is a sterol of vitamin D that, when converted in the liver into the active form, causes renal failure, cardiac abnormalities, hypertension, central nervous system depression, and gastric system distress (anorexia, vomiting, and constipation). Zinc phosphide is an inorganic rodenticide that converts to phosphine gas in the stomach, causing gastrointestinal distress (including vomiting and pain), hypotension, and cardiovascular collapse. See Table 1 (below) for the half-lives of rodenticides in the blood and liver of rats.

Table 1. Half-life (in days) of a single dose of rodenticides in the blood and liver of rats[1, 2].

Class of Rodenticide	Rodenticide	Dose (mg ai/kg)	Half-life (in days) in Blood	Half-life (in days) in Liver
Second Generation Anticoagulant Rodenticides	Brodifacoum	0.02 to 0.35	6.5 to 91.7[7]	113.5[3] to 350
	Bromadiolone	0.2 to 3.0	1.0 to 2.4	170 to 318
	Difenacoum[4]	1.2	NA	118
	Difethialone	0.5	2.3	126
First Generation Anticoagulant Rodenticides	Chlorophacinone	4 to 5	0.4	Less than 2
	Diphacinone	0.32	NA	Between 2 and 3[1, 3]
	Warfarin	NA[9], 1[3]	0.7 to 1.2[1]	7[1] to 26.2[3]
Non-anticoagulant Rodenticides[2]	Bromethalin[5]	NA[9]	5.5	NA
	Cholecalciferol[6]	NA[9]	1	~19[8]

1 Data summarized from Erickson and Urban, 2004, except where noted.
2. Data is not available for zinc phosphide, so it is not included on the chart.
3. Fisher et al, 2003.
4. U.S. EPA, 2007.
5. Spaulding and Spannring, 1988.
6. Marrow, 2001.
7. Vandenbroucke et al, 2008.
8. Body half-life (instead of liver half-life).
9. NA is defined as Not Available.

In 1999, CDFG requested that DPR place pesticide products containing the second generation anticoagulant rodenticide brodifacoum into reevaluation based on concerns regarding adverse effects to non-target wildlife. (Reevaluation is a process that allows DPR to evaluate the human health and environmental impacts of currently registered pesticide products.) After evaluating the data on file, DPR presented an issue paper recommending a number of mitigation measures and proposed that rodenticide baits containing brodifacoum, bromadiolone, and difethialone (difenacoum was not yet registered) be restricted to indoor structural use only. However, based on comments from representatives of the pest control industry expressing concern over the restriction, including comments from food processors noting that federal law requires rodent control to take place outside the building, DPR reconsidered its proposal.

DPR then became aware that the U.S. EPA was conducting risk assessments on numerous rodenticides. DPR decided to focus its reevaluation in coordination with U.S. EPA. In 2004, U.S. EPA (listed as Erickson and Urban, 2004) completed its *Potential Risks of Nine Rodenticides to Birds and Nontarget Mammals: a Comparative Approach*. In May 2008, U.S. EPA announced its final *Risk Mitigation Decision for Ten Rodenticides (RMD)*. At the time, all ten rodenticides came in various bait forms, including loose grains, pellets, and place packs, and only required the use of a bait station if the product could not be applied in locations out of reach of children. Most second generation anticoagulant rodenticides were labeled for use to control rats and mice in and around homes, industrial, commercial, agricultural and public buildings, transport vehicles, and similar structures in urban areas. In addition to being labeled to control commensal rodents around homes, industrial sites, etc., first generation anticoagulants were labeled for agricultural uses, below-ground mole and pocket gopher control and vole control. While both first and second generation anticoagulant rodenticide were labeled for the residential marketplace, second generation anticoagulant rodenticides had the bulk of the residential market share.

The RMD describes U.S. EPA's risk mitigation decision for rodenticide products containing the following ten active ingredients: brodifacoum, bromadiolone, bromethalin, chlorophacinone, cholecalciferol, difenacoum, difethialone, diphacinone (and its sodium salt), warfarin (and its sodium salt), and zinc phosphide. The RMD includes two major components: (1) reducing children's exposure to rodenticide products used in the home, and (2) reducing wildlife exposures and ecological risks. To minimize children's exposure to rodenticide products used in homes, U.S. EPA's RMD requires that all rodenticides intended for use above ground by residential consumers be sold as solid formulations with a bait station. To reduce wildlife exposures and ecological risks, U.S. EPA imposed sales, package size, and use site restrictions to reduce the availability of second generation anticoagulant products to the residential consumer market. The RMD also requires the use of bait stations for most outdoor, above-ground uses of the ten rodenticides.

The terms and conditions of sale/distribution specified in the RMD and in U.S. EPA's notice of registration/reregistration prohibit the sale of second generation anticoagulant rodenticides in stores oriented towards residential consumers such as grocery, drug, hardware, home improvement stores, and other standard retail outlets. Sale and distribution of the products were restricted to agricultural, farm, and tractor stores or directly to pest control operators and other professional applicators. In addition, according to U.S. EPA's RMD, second generation anticoagulant products can only be sold in packages that contain eight or more pounds of bait. Products containing eight to sixteen pounds of bait are labeled only for use inside and within 100 feet of agricultural buildings and man-made agricultural structures vulnerable to rodent infestations. These products cannot be used in and around homes and residential sites. Products labeled for 16+ pounds of bait can be used in and within 100 feet of man-made structures (including homes and other residential areas) that are vulnerable to rodent infestations. The RMD initially restricted use to within 50 feet from buildings, but in a U.S. EPA memo dated March 14, 2012, the distance for all non-homeowner rodenticide products was increased to 100 feet and the definition of "building" was expanded to include man-made structures such as trash receptacles which are often placed farther than 50 feet from buildings. As stated above, these larger size quantities of second generation rodenticides are intended for distribution and sale at agricultural, farm, and tractor stores or directly to pest control operators and other professional applicators. The intent is to remove the product from general consumer access, while still having the products available to poultry and livestock producers and professional users, such as licensed pest control applicators. However, in California, numerous homeowners live on the urban/rural edge and in rural areas on “ranchette” style properties (one to five acres of land per home). Due to the location and size of their property, people living in these areas, including ranchette owners, may shop at farm stores for supplies. Under current federal requirements, such individuals could purchase and use the 8 to 16 pound plus quantities of second generation anticoagulant rodenticides, even though they are not a “professional pesticide user.”

It is also important to note that not all second generation anticoagulant registrants complied with U.S. EPA’s mitigation measures. Six second generation anticoagulant products, targeted for the residential consumer market, are still registered for sale in California to residential consumers in grocery, drug, hardware, home improvement stores, and other standard retail outlets. On November 2, 2012, U.S. EPA took steps under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) to cancel these noncompliant products by issuing a draft Notice of Intent to Cancel and convening a FIFRA Scientific Advisory Panel (SAP) at the end of November 2012. On February 5, 2013, the U.S. EPA issued a “Notice of Intent to Cancel Registrations of, and Notice of Denial of Applications for, Certain Rodenticide Bait Products”. However, to date, the outcome of these federal actions has not been determined. In addition, U.S. EPA existing stocks provisions for all consumer-use second generation anticoagulant rodenticides allow continued sale of such products from consumer oriented retail stores until supplies are exhausted.

A review of current California registered rodenticide labels shows that first generation anticoagulant and non-anticoagulant rodenticides are available to, and for use by, residential consumers (only in packages ≤ 1 pound of bait) to control rats and mice indoors and outdoors within 50 feet of homes or buildings. These consumer based products must be in a block/solid formulation, and be sold with, and used in, a bait station. First generation anticoagulant and non-anticoagulant products geared towards professional users (≥4 pounds of bait) can be used in and within 100 feet of buildings (including residential buildings) and inside of transport vehicles. For these products, bait stations are required for all outdoor, above-ground uses and indoors where children, pets, or non-target wildlife may be exposed. Some of these products are also labeled for baiting of rat burrows.

DPR also registers first generation anticoagulant and non-anticoagulant rodenticides that are labeled for use outdoors for manual below-ground burrow baiting to control pocket gophers and moles. Rodenticides containing diphacinone and chlorophacinone, and the non-anticoagulant rodenticide zinc phosphide have approved uses to control ground squirrels. Certain chlorophacinone, diphacinone, and zinc phosphide products can also be used in agricultural areas (orchards, fields, as well as landscaped areas such as parks and golf courses) and as tracking powders. However, all agricultural and tracking powder uses are designated as restricted use pesticides and can only be purchased and used by a California certified/licensed applicator or under their direct supervision. Liquid formulations of diphacinone sodium salt can be diluted and used indoors in non-residential areas by professional applicators.

DPR currently registers 72 end use products containing second generation anticoagulant rodenticides. As mentioned above, there are six second generation anticoagulant products targeted for use by homeowners in and around homes. Of the remaining 66 second generation anticoagulant rodenticide products currently registered, about half are labeled for use only inside and within 100 feet of agricultural buildings and other man-made agricultural structures. The other half are labeled for use inside and within 100 feet of man-made structures such as homes, food processing facilities, industrial and commercial buildings, trash receptacles, agricultural and public buildings, and transport vehicles and are intended for use by professional applicators (such as pest control operators, public health officials, federal, state, and municipal employees charged with rodent control). Certain products are also labeled for use in rodent burrows, alleys, and sewers. Bait stations must be used indoors when children, domesticated animals, or non-target wildlife may be exposed. Bait stations are required for all outdoor, above ground placements. Currently, there are no second generation anticoagulant rodenticides labeled for agricultural field use.

Evaluated Data

DPR considered data from multiple sources, including CDFG, private agencies and individuals, and available journal articles and other resources. Utilizing all of these resources, DPR was able to obtain information on almost 1,300 animals.

From that data set, DPR removed approximately half of the animals and multiple studies because the data were collected from outside California and placed the information in Appendix I. From the remaining 630 California animals, DPR removed an additional 41 animals (including 37 geese, 3 other birds, and 1 mammal) because all were related to a specific incident where chlorophacinone was used in artichoke fields after chopping or cut-back of artichoke plants. To address the problem, the product's label was amended to prohibit the application of chlorophacinone "for a period of 30 days before or after chopping or cut-back of artichoke plants." DPR also removed 26 rodents (including Norway (or brown) rats, roof (or black) rats, "rats" without a specified species, and all mice) as these are "target" animals. Four hawks, and a fox were also removed because only summary data were available (i.e., results on individual animals and for the individual rodenticides were not available. A snake (which contained difethialone) and a bobcat fetus (which contained residues of brodifacoum and diphacinone) were removed because there are no standards (i.e., LD_{50} data on reptiles or bobcat fetus) against which to compare these animals. In addition, in each case only a single individual was available. When making scientific assessments, one usually wants data on more than one individual in order to assure that the data are not an anomaly. DPR placed summary information regarding the above animals in Appendix II. Also not included in DPR's main analysis are data on 58 fishers and 6 badgers that only recently became available. This new data is summarized in Appendix III.

Even though for scientific or timing reasons, DPR did not include the animals identified above in its main data analysis, the data still provide important information, and therefore, are summarized in Appendices I, II, and III.

DPR included all of CDFG's data in its main analysis, even though, in some cases, CDFG only reported animals that were positive for rodenticide residues (i.e., negative animals were excluded and the total number of animals analyzed was unknown). While including all of the CDFG data may result in an over representation of positive samples, DPR believes that the data provide value and do not over represent positive values for second generation anticoagulant rodenticides. Of the 492 animals included in DPR's analysis, 350 were from data sets that included both negative and positive samples. DPR compared the two data sets using statistical analysis (Chi-squared and Fisher's Exact with a level of significance of 0.05; using Preacher (2001)), and determined that the data sets (in regards to the second generation anticoagulant rodenticides, using the number of samples) are not significantly different. Therefore, DPR is comfortable including all CDFG data in its analysis.

Analysis

The data included in this analysis were collected between 1995 and 2011, and came from the following: WildCare's data (WildCare (2011)), CDFG's data (CDFG (2011), CDFG (2012a), CDFG (2012b)), and McMillin et al (2008)), Lima and Salmon's paper (Lima and Salmon (2010) and Lima and Salmon (2012)), Seth Riley's coyote data (Riley (2012)), and Riley et al's paper (Riley et al (2007)). The analysis includes 492 non-target animals (including 194 birds (primarily raptors) and 298 mammals (primarily San Joaquin kit fox, bobcats, mountain lions, coyotes, and foxes)).

The livers (and/or blood, in a few cases) of each animal were analyzed for at least six anticoagulant rodenticides. The animals were analyzed for the first generation - warfarin, chlorophacinone, and diphacinone - and second generation - brodifacoum, bromadiolone, and difethialone - anticoagulant rodenticides. In some cases, additional analyses were conducted, and those were reported where applicable. Two rodenticides not registered for use in California were also found, but will not be discussed. Those were coumachlor and pindone. In addition, because of its relatively recent entry into the rodenticide market, none of the 492 animals included in DPR's analysis were tested for difenacoum residues. Therefore, the lack of data showing difenacoum residues in animals is not indicative of a lack of toxicity.

Of the 492 non-target animals analyzed, approximately 75% had residues of one or more rodenticide, approximately 73% (359) had residues of at least one second generation anticoagulant rodenticide, and approximately 25% (124) were negative.

Brodifacoum residues were found in approximately 69% of the animals, bromadiolone residues were found in approximately 37% of the animals, and difethialone residues were found in approximately 8% of the animals. Of the animals that tested positive for at least one rodenticide, approximately 98% had residues of at least one second generation anticoagulant rodenticide. Table 2 summarizes these results.

Table 2. Number (and percent) of the rodenticides among all animals (n=492) and among the positive animals (n=368)[1].

Total	Number	Second Generation Anticoagulant Rodenticides			First Generation Anticoagulant Rodenticides		
Samples	492	359 (72.9%)			65 (13.2%)		
Positives	368	359 (97.6%)			65 (17.7%)		
Total	Number	Brodifacoum	Bromadiolone	Difethialone	Chlorophacinone	Diphacinone	Warfarin
Birds	194	124 (63.94%)	42 (21.7%)	10 (5.2%)	1 (0.5%)	5 (0.3%)	0 (0.0%)
Mammals	298	215 (72.2%)	141 (47.3%)	31 (10.4%)	17 (5.7%)	48 (16.1%)	4 (1.3%)
Total	492	339 (68.9%)	183 (37.2%)	41 (8.3%)	18 (3.7%)	53 (10.8%)	4 (0.8%)
Positives	368	339 (92.1%)	183 (49.7%)	41 (11.1%)	18 (4.9%)	53 (14.4%)	4 (1.1%)

[1] Animals may be positive for more than one rodenticide.

This table indicates that exposure of non-target animals to second generation anticoagulant rodenticides far exceeds exposure to first generation anticoagulant rodenticides. In addition, brodifacoum residues were found in a large percentage of the animals (almost 70%).

Tables 3 and 4 show the bird and mammal data down to the species level.

Table 3. Number of each bird (n=194) species that was positive for a rodenticide, that was positive for a first or second generation anticoagulant rodenticide, and that was for each rodenticide[1].

Species	n	Positive	2nd generation	Brodifacoum	Bromadiolone	Difethialone	1st generation	Chlorophacinone	Diphacinone	Warfarin
American Crow	1	1	1	1	0	0	0	0	0	0
American Kestrel	6	5	4	3	0	1	1	0	1	0
Bald Eagle	1	1	0	0	0	0	1	0	1	0
Barn Owl	49	29	29	28	15	2	0	0	0	0
Black Crowned Night Heron	1	0	0	0	0	0	0	0	0	0
Brown Pelican	2	0	0	0	0	0	0	0	0	0
Burrowing Owl	1	0	0	0	0	0	0	0	0	0
Canada Goose	1	0	0	0	0	0	0	0	0	0
Cooper's Hawk	17	14	14	14	3	0	1	0	1	0
Dark eyed junco	1	0	0	0	0	0	0	0	0	0
Golden Eagle	11	8	8	8	0	0	0	0	0	0
Great Horned Owl	21	17	17	16	8	1	1	0	1	0
Gull (any)	3	0	0	0	0	0	0	0	0	0
Hawk (unknown species)	1	1	1	1	1	1	0	0	0	0
Long-eared Owl	1	1	1	1	0	0	0	0	0	0
Northern Harrier	1	0	0	0	0	0	0	0	0	0
Prairie Falcon	1	0	0	0	0	0	0	0	0	0
Red-shouldered Hawk	22	17	16	16	8	1	0	0	0	0
Red-tailed Hawk	32	23	23	22	5	3	1	1	0	0
Sharp-shinned Hawk	9	6	6	6	0	1	0	0	0	0
Spotted Owl	2	1	1	1	0	0	0	0	0	0
Swainson's Hawk	1	1	1	1	0	0	0	0	0	0
Turkey Vulture	6	5	5	5	2	0	1	0	1	0
Western Screech Owl	3	1	1	1	0	0	0	0	0	0
Total	194	131	128	124	42	10	6	1	5	0

1. Animals may be positive for more than one rodenticide.

Table 4. Number of each mammalian (n=298) species that was positive for a rodenticide, that was positive for a first or second generation anticoagulant rodenticide, and that was for each rodenticide[1].

Species	N	Positive	2nd generation	Brodifacoum	Bromadiolone	Difethialone	1st generation	Chlorophacinone	Diphacinone	Warfarin
Badger	3	1	0	0	0	0	1	1	1	0
Black Bear	3	3	3	3	3	0	2	2	2	0
Bobcats	41	36	35	31	26	11	15	1	13	1
Coyotes	44	36	33	33	12	4	8	4	6	1
Deer	1	0	0	0	0	0	0	0	0	0
Gray fox	9	7	7	7	4	1	2	0	2	0
Mountain Lions	28	28	28	27	26	11	18	3	17	2
Pig (Feral)	1	1	0	0	0	0	1	0	1	0
Raccoons	6	4	4	4	4	0	1	0	1	0
Red fox	37	35	35	30	25	2	4	0	4	0
San Joaquin kit fox	110	76	76	70	35	2	7	6	1	0
Skunk (any)	7	5	5	5	4	0	0	0	0	0
Squirrel (any)	5	2	2	2	0	0	0	0	0	0
Virginia Opossum	3	3	3	3	2	0	0	0	0	0
Total	298	237	231	215	141	31	59	17	48	4

1. Animals may be positive for more than one rodenticide.

Comparisons to Wildlife LD_{50}s

A LD_{50} is the dose (in mg/kg of body weight) of a chemical that a species consumes in a single dose that is lethal to 50% of the animals of that species tested. A LC_{50} is the concentration (in parts per million (ppm) or as mg/kg of body weight/day) of a chemical that produces mortality in 50% of the animals to which it is exposed (normally in the air, water, or food) in a given period of time. U.S. EPA has established guidelines for the LD_{50}s and LC_{50}s.

Table 5. Descriptive toxicity categories for wildlife compared to the LD_{50}s and LC_{50}s.

Descriptive Term	Mammal and Avian LD_{50}	Mammal and Avian LC_{50}
Extremely Toxic	< 10 mg/kg	< 50 ppm
Highly Toxic	10 – 50 mg/kg	50 – 500 ppm
Moderately Toxic	50 - 500 mg/kg	500 – 1,000 ppm
Slightly Toxic	500 – 2,000 mg/kg	1,000 – 5,000 ppm
Relatively Non-Toxic	> 2,000 mg/kg	> 5,000 ppm

Based on these descriptive categories, a rodenticide that is "extremely toxic" is toxic to 50% of the animals of that species tested at <10mg/kg of the chemical. However, there can be an apparent difference in sensitivities in the LD_{50}s between species and even individuals. For example, the most sensitive LD_{50} for brodifacoum is 0.26 mg/kg, is in a mallard. However, the Ring-necked pheasant has an LD_{50} of 10 mg/kg (Erickson and Urban, 20004).

To equilibrate all of the finding, the most sensitive LD_{50}s were used. Table 6 lists the LD_{50}s and the descriptive toxicities (based on the U.S. EPA's Pesticide Assessment Guidelines) for the nine rodenticides for the most sensitive birds and mammals.

Table 6. Most sensitive LD_{50} and descriptive toxicity[1] for birds and mammals for nine rodenticides[2].

Type of Rodenticide	Rodenticide	Most sensitive LD_{50} for Birds (in mg/kg)	Descriptive Toxicity for the most sensitive Birds LD_{50}	Most sensitive LD_{50} for Mammal (in mg/kg)	Descriptive Toxicity for the most sensitive Mammal LD_{50}
Second Generation Anticoagulant Rodenticides	Brodifacoum	0.26	Extremely Toxic	0.13	Extremely Toxic
	Bromadiolone	138	Moderately Toxic	0.56	Extremely Toxic
	Difenacoum	66[3]	Moderately Toxic	0.45[3]	Extremely Toxic
	Difethialone	0.26	Extremely Toxic	0.29	Extremely Toxic
First Generation Anticoagulant Rodenticides	Chlorophacinone	>100	Moderately Toxic	0.49	Extremely Toxic
	Diphacinone	96.8[4]	Moderately Toxic	0.2	Extremely Toxic
	Warfarin	620	Slightly Toxic	2.5	Extremely Toxic
Non-Anticoagulant Rodenticides	Bromethalin	4.6	Extremely Toxic	2.0	Extremely Toxic
	Cholecalciferol	>600	Slightly Toxic	5.5	Extremely Toxic
	Zinc phosphide	8.8	Extremely Toxic	26	Highly Toxic

1. From the EPA Pesticide Assessment Guidelines (U.S. EPA, 2011).
2. Data summarized from Erickson and Urban, 2004, except where noted.
3. U.S. EPA, 2007.
4. Rattner et al, 2011.

The data indicate that the second generation anticoagulant rodenticides brodifacoum and difethialone are extremely toxic to both birds and mammals. The second generation anticoagulant rodenticides bromadiolone and difenacoum are moderately toxic to birds, but extremely toxic to mammals.

It is important to note that LD_{50} tests are run in a laboratory setting, where the animals are not subject to the need to forage, or to predation or pathogen pressures. Additionally, the LD_{50} considers only one endpoint: mortality. Multiple studies (Eason et al (1996), Fisher (2009), and Naz et al (2011)) have shown that even sub-lethal doses can cause clotting, biochemical (including glucose and liver function markers), and physiological abnormalities (including statistically significant decreased body weight, increased liver size, increased heart size, and increased kidney size), which could or did cause mortality in the laboratory setting.

Field and epidemiological studies can provide additional information about what happens in non-laboratory situations. Dowding et al (1999) analyzed brodifacoum concentrations in the livers of cats, rabbits, and birds found dead or euthanized on Motuihe Island following a Norway rat and house mouse eradication operation in August 1997. Three cats found dead had liver brodifacoum concentrations of 0.91 to 1.38 ppm. Five rabbits found dead on the island had liver concentrations of 0.05 to 2.01 ppm. Twenty-nine non-target birds (including ducks, raptors, and songbirds) that were found dead had liver concentrations of 0.12 to 2.31 ppm. The incidence of mortality 2 weeks after the eradication was 49% in the pukeko flock (order: Gruiformes; a coot) and 60% in the paradise shelduck flock (order: Anseriformes; a duck). It is likely, given their behavior and eating habits, that the rabbits and paradise shelduck directly consumed the bait, while the cats and raptors would most likely have consumed prey items that had consumed the bait. Depending upon the species, circumstances, and individual involved, the songbirds and pukeko may have directly consumed the bait and/or consumed prey that consumed the bait.

Riley et al (2007) found that all 19 of the bobcats that died due to severe notoedric mange were exposed to second generation anticoagulant rodenticides, with brodifacoum ranges from trace to 0.56 ppm. Morbidity or mortality due to notoedric mange had not previously been reported as a significant pathogen in wild felid. The study demonstrated that where the levels of second generation anticoagulant rodenticides were more than 0.05 ppm, the correlation to mange (and mortality) was "highly significant" with a p-value < 0.01.

In the laboratory, second generation rodenticides are also known to cause lethargy, shortness of breath, anorexia, bloody diarrhea, changes in behavior, potential heart damage, and tenderness of the joints (Cox and Smith (1992), Housenger and Melendez (2011), IPCS (2010), Littin et al (2000), Merck Sharp & Dohme Corp (2011), Munday and Thompson (2003), Naz et al (2011), Rahmy (1993), Shlosberg and Booth (2001), Valchev (2008), and Woody et al (1992)). Therefore, even sub-lethal exposure to anticoagulants may contribute to the ill thrift of the animal. U.S. Fish and Wildlife Service (2010) stated that, "Even in cases where the proximate cause of death has been identified as automobile strike, predation, or disease, toxicologists and pathologists have attained sufficient toxicological evidence to conclude that rodenticide-induced blood loss increased animal vulnerability to the proximate cause of death."

The concentration of brodifacoum in the liver (which is in ppm), while not always an accurate reflection of the amount of brodifacoum ingested (which is in mg/kg), demonstrates exposure and when a necropsy is conducted, is often used in conjunction with everything else to assess the potential mortality based on the liver residues of the rodenticide. For example, Eason et al (1996) dosed the Common Brushtail Possum (*Trichosurus vulpecula*) with 0.1 mg/kg and found mean liver concentrations of 0.100 ppm 14 days after dosing, 0.109 ppm 63 days after the dosing, and 0.075 ppm 126 days after dosing. Fisher et al (2003) dosed rats with 0.1 mg/kg brodifacoum and found the mean liver residue concentration after one week to be 1.27 ppm, after 18 weeks to be 0.59 ppm, and after 24 weeks to be 0.49 ppm. Additionally, Eason et al (1999) dosed pigs with brodifacoum in single dietary doses of 0.57 ppm, 0.96 ppm, and 1.94 ppm and then analyzed their livers on the fifth day. When the pigs consumed approximately 0.57 mg/kg, 0.96 mg/kg, and 1.94 mg/kg, the resulting brodifacoum concentration in the liver was 1.13 ppm, 1.08 ppm, and 1.05 ppm, respectively. If the whole body concentration of brodifacoum were analyzed, instead of the just the concentration in the liver, the concentration would be significantly lower. Because the liver essentially collects the rodenticide, the liver is analyzed, which allows for the determination of exposure. However, because the liver collects the rodenticide, the rodenticide can be found at a higher concentration in the liver than in the animal at a whole.

Of the 492 animals included in this analysis, 368 (approximately 75%) had residues of at least one first and/or second generation anticoagulant rodenticide. Table 7 quantifies the number and percent of samples that had residues (including trace residues), those which had measurable (i.e., non-trace) residues, and those which had residues above the most sensitive LD_{50}.

Table 7. Number (and percent) of animals that had anticoagulant rodenticide residues (including trace residues), had measurable (i.e., non-trace) residues, and that had anticoagulant levels above the most sensitive LD_{50} (n=492)[1].

Rodenticide		Avian	Mammal	Total
Any	Total Number of samples	194 (100%)	298 (100%)	492 (100%)
	Total Number with no residues[2]	63 (32.5%)	61 (20.5%)	124 (25.2%)
	Total Number of positive samples[3]	131 (67.5%)	237 (79.5%)	368 (74.8%)
Brodifacoum	Total Number with no residues[2]	70 (36.1%)	83 (27.9%)	153 (31.1%)
	Total Number of positive samples[3]	124 (63.9%)	215 (72.1%)	339 (68.9%)
	Number with measurable residues[4]	107 (55.2%)	199 (66.8%)	306 (62.2%)
	Number above the most sensitive LD_{50}[5]	26 (13.4%)	85 (28.5%)	111 (22.6%)
Bromadiolone	Total Number with no residues[2]	152 (78.4%)	157 (52.7%)	309 (62.8%)
	Total Number of positive samples[3]	42 (21.6%)	141 (47.3%)	183 (37.2%)
	Number with measurable residues[4]	26 (13.4%)	111 (37.2%)	138 (28.0%)
	Number above the most sensitive LD_{50}[5]	0 (0.0%)	38 (12.8%)	38 (7.7%)
Difethialone	Number with no residues[2]	184 (94.8%)	267 (89.6%)	451 (91.7%)
	Total Number of positive samples[3]	10 (5.2%)	31 (10.4%)	41 (8.3%)
	Number with measurable residues[4]	5 (2.6%)	4 (1.3%)	9 (1.8%)
	Number above the most sensitive LD_{50}[5]	5 (2.6%)	4 (1.3%)	9 (1.8%)
Chlorophacinone	Number with no residues[2]	193 (99.5%)	250 (83.9%)	439 (89.3%)
	Total Number of positive samples[3]	1 (0.5%)	17 (5.9%)	18 (3.7%)
	Number with measurable residues[4]	0 (0.0%)	11 (3.7%)	11 (2.2%)
	Number above the most sensitive LD_{50}[5]	0 (0.0%)	3 (1.0%)	3 (0.6%)
Diphacinone	Number with no residues[2]	189 (97.4%)	250 (83.9%)	439 (89.3%)
	Total Number of positive samples[3]	5 (2.6%)	48 (16.1%)	53 (10.8%)
	Number with measurable residues[4]	3 (1.5%)	17 (5.7%)	20 (4.1%)
	Number above the most sensitive LD_{50}[5]	2 (1.0%)	10 (3.4%)	12 (2.4%)
Warfarin	Number with no residues[2]	194 (100.0%)	294 (98.7%)	488 (99.2%)
	Total Number of positive samples[3]	0 (0.0%)	4 (1.3%)	4 (0.8%)
	Number with measurable residues[4]	0 (0.0%)	2 (0.7%)	2 (0.4%)
	Number above the most sensitive LD_{50}[5]	0 (0.0%)	0 (0.0%)	0 (0.0%)

1. Animals may be positive for more than one rodenticide.
2. The number of samples with no residues is the number of samples that did not have trace or measurable amounts in it. It can be added to the Number of Total Number of positive samples to get the Total Number of samples.
3. The samples that tested positive for a sample may have had trace (i.e., when the rodenticide is known to be present but its level is so low that it cannot be quantified) or measurable (i.e., when the amount of a rodenticide can be put into a number) amounts of the rodenticide. It can be added to the Number of samples with no residues to get the Total Number of samples.
4. The number of samples with measurable or quantifiable residues includes only the samples where the amount of a rodenticide can be put into a number (i.e., it does not include the trace detections). This is part of the Total Number of

positive samples, but does not include the trace samples (i.e., the Total Number of positive samples minus Number with measurable residues will equal the number with trace residues). For this reason, this number should not be added to any of the other categories.

5. The number of samples above the LD_{50} includes only those samples that have measurable residues and that are above the most sensitive LD_{50} (a measurable amount) for the species (listed in Table 6). This is part of the Number with measurable residues, but lacks those that are not above the LD_{50} (i.e., the Number with measurable residues minus the Number above the most sensitive LD_{50} will equal the number that fell between those that had measurable detections and those that were above the LD_{50}). For this reason, this number should not be added to any of the other categories.

This table indicates that number of non-target animals that had second generation anticoagulant rodenticide residues (including trace residues), had measurable (i.e., non-trace) residues, and that had anticoagulant levels above the most sensitive LD_{50} (n=492)[1] exceeds the numbers for first generation anticoagulant rodenticides. Brodifacoum residues were found in approximately 69% of samples and in those samples brodifacoum residues were above the most sensitive LD_{50} approximately 23% of the time. Bromadiolone residues were found in approximately 37% of samples and in those samples bromadiolone residues were above the most sensitive LD_{50} approximately 8% of the time. Difethialone residues were found in approximately 8% of samples and in those samples difethialone residues were above the LD_{50} approximately 2% of the time. While liver residues above the LD_{50} (or sometimes even below) indicates that some of these animals could have died due to the concentrations of the rodenticide seen in their liver, it is difficult to definitely correlate exposure to the cause of death of an individual, without evidence of coagulopathy at necropsy.

Necropsies

Out of the 492 animals analyzed, 211 necropsies (including 124 birds and 87 mammals) were conducted. The 80 necropsies presented to DPR for evaluation were conducted by veterinarians (including both those with advanced training in pathology and those without advanced training in pathology) and non-veterinarians, and were assessed accordingly. The remaining necropsies were present in Lima and Salmon's and Riley et al's papers.

Multiple difficulties can arise when conducting a necropsy, including a freeze-thaw artifact, a decomposing body, and/or if predated body. In many cases, necropsies on animals with these problems were excluded or were assessed more carefully.

Of the 211 necropsies, 38 (approximately 19%) indicate that anticoagulant rodenticides contributed to or could be correlated to morbidity (i.e., disease), but were not the cause of death, or more information or analysis was needed to establish the cause of death. Thirty-three (33) of the necropsies (approximately 16%) indicate that anticoagulant rodenticides were likely a cause of death or the cause of death. Of the 33 cases where anticoagulant rodenticides were the most likely cause of death, second generation rodenticides were involved in 29 cases (approximately 14%). Specifically, brodifacoum was involved in 28 cases (approximately 13%), and brodifacoum was likely the sole or primary cause of death in 20 cases (approximately 9%).

Additionally, bromadiolone was involved in 7 cases (approximately 3%). Table 8 summarizes the results.

Table 8. Summary of the rodenticides identified as the likely cause of death (based on the analysis of the necropsies), the concentration(s) of the individual rodenticide(s), and the total rodenticides concentration in the liver of the animal.

Birds (n=124)	Mammals (n=87)	Number (n=211)	Primary Rodenticide(s) Involved	Rodenticide Concentration (ppm)	Total Rodenticide Concentration
9 (7.3%)	11 (12.6%)	20 (9.5%)[1]	Brodifacoum	Trace to 11.0	Trace to 11.0
4 (3.2%)	2 (2.3%)	6 (2.8%)[2]	Brodifacoum Bromadiolone	0.07 to 0.57 0.065 to 1.27	0.38 to 1.84
1 (0.8%)	0 (0.0%)	1 (0.5%)[3]	Bromadiolone	0.38	0.38
1 (0.8%)	1 (1.1%)	2 (1.0%)[4]	Brodifacoum Diphacinone	0.002 to 0.08 0.169 to 1.30	0.171 to 1.38
2 (1.6%)	0 (0.0%)	2 (1.0%)[5]	Diphacinone	Trace to 3.5	Trace to 3.5
0 (0.0%)	2 (2.3%)	2 (1.0%)[6]	Chlorophacinone	0.4 to 1.2	0.4 to 1.2
17 (13.7%)	16 (18.4%)	33 (15.6%)[7]	Total		

1. The 9 birds were a Cooper's Hawk, a Turkey Vulture, 2 Barn Owls, 2 Great Horned Owls, and 3 Golden Eagles. The 11 mammals were a mountain lion, an opossum, a red fox, an endangered San Joaquin kit fox, 2 bobcats, 2 fox squirrels, and 3 coyotes.
2. The 4 birds were 2 Barn Owls and 2 Great Horned Owls. The 2 mammals consisted of 2 mountain lions.
3. The bird was a Barn Owl.
4. The bird was a Barn Owl. The mammal was a coyote.
5. The 2 birds were a Bald Eagle and Turkey Vulture.
6. The 2 mammals were a coyote and a bobcat.
7. The 17 birds were a Bald Eagle, a Cooper's Hawk, 2 Turkey Vultures, 3 Golden Eagles, 4 Great Horned Owls, and 6 Barn Owls. The 16 mammals were an opossum, a red fox, an endangered San Joaquin kit fox, 2 fox squirrels, 3 bobcats, 3 mountain lions, and 6 coyotes.

Of the 29 necropsies where second generation anticoagulant rodenticides were the likely cause of death, the overall levels of second generation anticoagulant rodenticides ranged from trace to 11.0 ppm. In the 20 cases where brodifacoum was the primary or sole compound that caused mortality, brodifacoum residues ranged from trace to 11.0 ppm.

Animal Information, Diet, and Habitat

The Migratory Bird Treaty Act of 1918 prohibits the take of native birds (including killing or causing the death of a bird) without a permit. Additionally, Bald and Golden Eagles are further protected by the Bald and Golden Eagle Protection Act of 1962. The majority of the birds analyzed in this paper are carnivores that are likely exposed to rodenticides either by secondary or tertiary exposure. The Barn Owl and the Great Horned Owl are nocturnal raptors. The Barn Owl prefers to hunt in open country and along the edges of woods (in rural and natural areas), but also lives in urban and suburban areas. They primarily eat rodents, but will also eat other small mammals, birds, and invertebrates (Rocha et al (2011) and Pezzo and Morimando (1995)). Great Horned Owls prefer wooded (natural) and forested areas, but will live in natural, suburban, rural and urban areas. They primarily eat small to medium mammals (such as rabbits, and rodents), but will also eat larger mammals, birds (including other raptors), reptile, amphibian, and fish (Marti and Kochert (1996)).

Bald Eagles, Cooper's Hawks, Golden Eagles, Red-shouldered Hawks, Red-tailed Hawks, and Turkey Vultures are diurnal raptors. Bald Eagles tend to live among trees near water, and prefer natural or rural areas (Guinn (2004)). They primarily eat fish, but will also eat carrion, mammals, avian (including other raptors), reptiles, amphibians, and invertebrates (Peterson (1986)). Cooper's Hawks are agile fliers that fly through thick cover (including trees, vegetation, and buildings) to catch its prey. They prefer wooded and forested areas, but live in urban, suburban, rural, and natural areas. They primarily prey upon on birds, but will also eat mammals (Roth and Lima (2003)). Golden Eagles prefer nesting on mountains and hunting in open areas, such as rural areas (non-agricultural) and natural areas (Carrette et al (2000) and Marzluff et al (1997)). They primarily eat rabbits and squirrels, but will take prey weighing 1 to 15 pounds, including mammals, birds (including other raptors), reptiles, amphibians, fish, insects, and carrion (Bloom and Hawks (1982), and Steenhof and Kochert (1998)). The Red-shouldered Hawk prefers to live in woodlands (natural areas), especially near rivers or swamps, but will live in suburban and rural areas. They primarily prey upon small mammals (especially rodents), but will also consume reptiles, amphibians, birds, and crayfish (Jacobs and Jacobs (2002)). The Red-tailed Hawk prefers to live in open (rural or natural) areas, but also live urban and suburban areas. They primarily prey upon rodents, but will also consume other mammals (including predators), birds (including other raptors), reptiles, amphibians, and insects (Gatto et al (2005), and Steenhof and Kochert (1998)). Turkey Vultures prefer open areas, such as rural and natural areas. Their diet is almost exclusively composed of carrion, including small and large mammals, birds, reptiles, and fish (Hiraldo et al (1991a) and Hiraldo et al (1991b)).

Some of the mammals analyzed in this paper included bobcats, mountain lions, coyotes, red foxes, San Joaquin kit foxes, fox squirrels, opossum, and skunks. Bobcats and mountain lions are solitary animals and strict carnivores (normally only eat meat). Mountain lions tend to found primarily in rural and natural areas. A mountain lion's diet is primarily composed of ungulates (primarily deer), although they will also eat rodents, insects, and predators (including coyotes), depending upon location, season, and abundance (Blakenship (1995), Iriarte et al (1990), and Riley et al (2007)). They are most likely to be exposed to rodenticides by tertiary (i.e., the animal eats an animal that ate an animal that ate the rodenticide) exposure, although secondary exposure is possible. Bobcats prefer woodland (natural areas), but will live in rural areas, in some suburban areas, as well as on the edges of urban areas. They primarily consume rodents and rabbits, although they will also consume insects, reptile, and larger prey (including deer), depending upon availability, season, and preference (Blakenship (1995) and Litvaitis (1981)). They are most likely to be exposed by secondary exposure, although tertiary exposure is possible.

Coyotes are a medium sized generalist predator that can live in urban, suburban, rural, or natural environments. They primarily eat small mammals (such as rodents, rabbits, and squirrels), but will also eat birds, snakes, deer, seed, and fruit (Blakenship (1995)). There are three red fox species in California: the Sacramento Valley red fox, the Sierra Nevada red fox, and the non-native red fox (Sacks et al (2010)). Although the subspecies can differ in distribution, appearance, and behavior, the red fox will, in general, live in urban, suburban, rural, and natural environments. They are crepuscular animals that primarily eat rodents, but their diet also includes birds, insects, other mammals (including other predators), small deer, fish, fruit, carrion, and refuse (Lariviere and Pasitschniak-Arts (1996), and Papakosta et al (2010)). The San Joaquin kit foxes are a small (approximately five pounds) canid that is federally listed as endangered. They are only found in the San Joaquin Valley and Central Coast of California, but they live in urban (including downtown Bakersfield), suburban, rural, and natural areas. They primarily eat rodents (including kangaroo rats), rabbits, and squirrels, but will also consume reptiles, insects, birds, carrion, fruit, and refuse (Frost (2005)), McGrew (1979)) and Warrick et al (2007)), depending upon season, availability, and location. Coyotes and foxes most likely ingest rodenticides secondarily (by ingesting a rodent or squirrel), although they could be exposed via tertiary exposure or by directly consuming it.

Fox squirrels prefer forested areas, but can be found in urban, suburban, rural, and natural environments. They consume tree seeds, tree buds, tree flowers, bird eggs, and mushrooms (Lee et al (2001)) and Koprowski (1994)). They are most likely exposed to rodenticides through direct ingestion. Virginia opossums are a marsupial. They can live in urban, suburban, rural, and natural environments. Opossums are opportunistic omnivores, eating insects, plants, fruit, mammals (dead or alive), birds, reptiles, and refuse (McManus (1974)). They are most likely exposed to rodenticides by direct consumption or secondary exposure. Skunks live in urban, suburban, rural, and natural areas. They are crepuscular omnivores that eat primarily insects, but will also eat vertebrates, carrion, eggs, fruit, leaves, grains, nuts, and refuse (Kasparian et al (2002) and Wade-Smith and Verts (1982)). They most likely ingest rodenticides by secondary exposure, but may also be exposed by tertiary exposure or direct ingestion the rodenticide.

Location & Land Use

Of the 492 animals, counties were provided for 491 of them and more precise locations (i.e., urban, rural, natural/wild area based on population and/or land use) were provided for 248 animals. DPR looked at the location where each of the animals analyzed were found to determine whether the animals were found in predominately urban, rural, or natural (wild areas) settings.

The 492 animals came from at least 35 California counties, including Alameda, Colusa, Contra Costa, El Dorado, Fresno, Glenn, Kern, Kings, Los Angeles, Madera, Marin, Mendocino, Merced, Monterey, Napa, Orange, Placer, Riverside, Sacramento, San Benito, San Bernardino, San Diego, San Francisco, San Joaquin, San Luis Obispo, San Mateo, Santa Clara, Santa Cruz, Sonoma, Solano, Stanislaus, Sutter, Tulare, Ventura, and Yolo.

The map below shows all the counties from which animals were analyzed.

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Figure 1. Counties in California from which animals were analyzed, as indicated by a ✚.

The data indicate that animal’s positive for anticoagulant residues were found in urban and rural settings, as well as nature preserves. For example, Lima and Salmon’s (2010) data indicate that residues of second generation anticoagulant rodenticides were found more often in raptors in San Diego County, than in raptors from the Central Valley. See Table 9.

Table 9. Number of raptors analyzed that had anticoagulant rodenticide residues (including trace residues) by region from 2006 to 2009 (n = 96 raptors)[1,2].

Region	Number of samples analyzed	Second Generation Anticoagulant Rodenticides			First Generation Anticoagulant Rodenticides		
		Brodifacoum	Bromadiolone	Difethialone	Chlorophacinone	Diphacinone	Warfarin
San Diego County	53	49 (92.4%)	22 (41.5%)	8 (15.1%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Central Valley	43	25 (58.1%)	5 (11.6.0%)	0 (0.0%)	1 (2.3%)	0 (0.0%)	0 (0.0%)
Total	96	75 (78.1%)	28 (29.2%)	8 (8.3%)	1 (1.0%)	0 (0.0%)	0 (0.0%)

1. Animals may be positive for more than one rodenticide.
2. Data differs from Lima and Salmon's Table 3.

In San Diego County, there was no statistical difference between the percentage of animals with residues of brodifacoum, bromadiolone, and difethialone in rural areas (as defined by population) and urban areas (using Preacher (2001)), even though bromadiolone residues were found in a higher percentage of urban samples than in the rural samples. See Tables 10 and 13, below.

Table 10. Number of raptors analyzed that had anticoagulant rodenticide residues (including trace residues) by population density/land use within San Diego County from 2006 to 2009 (n=53 raptors) [1,2].

Population Density	Number of Animals	Brodifacoum	Bromadiolone	Difethialone
Urban	17	16 (94.1%)	9 (52.9%)	3 (17.6%)
Unknown	1	0 (0.0%)	0 (0.0%)	0 (0.0%)
Rural	35	33 (94.3%)	13 (37.1%)	5 (14.3%)
Total	53	49 (92.5%)	22 (41.5%)	8 (15.1%)

1. Samples may be positive for more than one rodenticide.
2. None of the samples were positive for a first generation anticoagulant rodenticide.

San Joaquin kit foxes are federally listed as an endangered species and state listed as threatened. According to the U.S. Fish & Wildlife Services, "“Endangered” means a species is in danger of extinction throughout all or a significant portion of its range." Although the number San Joaquin kit fox living in Bakersfield *might* be as high as 400 individuals, this number has not been deemed sufficient to keep them from going extinct, especially since "a century ago, more than 12,000 if the foxes roamed the San Joaquin Valley (Cypher (2010))."

In their "5-Year Review: Summary and Evaluation" the U.S. Fish and Wildlife Service (2010) found that

> Pesticides, and specifically rodenticides, pose a threat to kit fox through direct or secondary poisoning. For example, kit fox may be killed if they ingest rodenticide

> in a bait application, or if they consume rodents that have consumed bait… Secondary exposure to SGARs is particularly problematic due to the high toxicity of the compounds and their long persistence in body tissues. For example, brodifacoum, a common SGAR, is persistent in tissue, bioaccumulates, and appears to impair reproduction… Even in cases where the proximate cause of death has been identified as automobile strike, predation, or disease, toxicologists and pathologists have attained sufficient toxicological evidence to conclude that rodenticide-induced blood loss increased animal vulnerability to the proximate cause of death (USEPA 2008)… the Service expects that effects of rodenticide exposure could have substantial population level effects where exposure is present, especially where kit fox populations are small and where they rely on target species, such as ground squirrels and murid rodents, for prey.

DPR found that of the samples, approximately 73% were positive for second generation anticoagulant rodenticides, and out of 110 San Joaquin kit foxes that were sampled, approximately 64% of the animals were positive for brodifacoum and approximately 33% were positive for bromadiolone, which includes 13 kit fox in the relatively isolated Lokern area (an isolated area where only animals had residues for bromadiolone). For instance, in 2009, of the 4 animals that were analyzed, all 4 were found in Bakersfield and 3 of the 4 had brodifacoum residues. And, in 2011, of the 4 animals that were analyzed, all 4 were found in Kern County and all 4 had brodifacoum and bromadiolone. Since 2009, 7 of the 8 animals (87.5%) have had second generation rodenticides, specifically brodifacoum. Additionally, there was likely at least 1 mortality that was most likely caused by brodifacoum. Of the approximately 400 animals in Bakersfield, this indicates that between 293 and 350 might have residues for a second generation rodenticide. Based on the analysis by U.S. Fish and Wildlife Service, the exposure to second generation anticoagulant rodenticides can cause take, including mortality, which could have "substantial population level effects" on an endangered species that is "in danger of extinction."

Additionally, of the 120 animals analyzed from the San Joaquin kit fox data (CDFG (2011) and CDFG (2012b)), including 110 San Joaquin kit fox, 1 badger, 1 bobcat, 2 coyotes, 2 skunks, and 4 red foxes, approximately 80% of the animals from Bakersfield (an urban area) had residues of brodifacoum. Only 30% of the animals had residues of brodifacoum from "other locations" in Kern, San Benito, San Luis Obispo, and Tulare counties (which could include urban, suburban, rural, agricultural, and/or natural areas) and none of the animals from Lokern (a 40,000 acre natural area, designed to provide quality brush scrub habitat for threatened and endangered plants and animals) had residues of brodifacoum. While, one animal collected from Lokern (in 2007) was positive for bromadiolone, there was a significant difference between the number of animals in the urban and rural areas that were positive for brodifacoum and bromadiolone. See Tables 11 and 13, below.

Table 11. Number of animals analyzed that had anticoagulant rodenticide residues (including trace residues) by location (land use and County) from 1999 to 2011 (n=120)[1,2].

Location (Land use/type)	County	Number	Second Generation Anticoagulant Rodenticides			First Generation Anticoagulant Rodenticides	
			Brodifacoum	Bromadiolone	Difethialone	Chlorophacinone	Diphacinone
Bakersfield (Urban)	Kern	75	60 (80.0%)	29 (38.7%)	0 (0%)	6 (8.0%)	2 (2.7%)
Unknown	Kern	10	7 (70.0%)	8 (80.0%)	2 (20.0%)	1 (10.0%)	0 (0%)
Other[3]	Various	20	6 (30.0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Lokern (Natural Area)	Kern	15	0 (0%)	1 (6.7%)	0 (0%)	0 (0%)	0 (0%)
Total		120	73 (60.8%)	38 (31.7%)	2 (1.7%)	7 (5.8%)	2 (1.7%)

1. Samples may be positive for more than one rodenticide.
2. None of the samples were positive for warfarin.
3. "Other" includes areas in Kern, San Benito, San Luis Obispo, and Tulare counties which could include urban, suburban, rural, agricultural, and/or natural areas.

Multiple studies have been conducted on coyotes, bobcats, and mountain lions, in Los Angeles and Ventura Counties, in urban and rural areas, including in the Santa Monica Mountains National Recreation Area (SMMNRA). The SMMNRA preserve is over 150,000 acres in the Santa Monica Mountains, between the Pacific Ocean and the inland valley. It contains many individual parks and open spaces, and is administered by the National Park Service (NPS), in conjunction with multiple state and local agencies and groups. While some parks and spaces within the park do not use second generation anticoagulant rodenticides, at least one facility in the NPS uses bromadiolone inside tamper-proof boxes (Miller, 2012).

Of the 28 mountain lions found in eight counties that were tested between 1997 and 2011, 100% tested positive for a second generation rodenticide, approximately 96% tested positive for brodifacoum, 93% tested positive for bromadiolone, and 39% tested positive for difethialone (almost all of the mountain lions were positive for more than one rodenticide). In their study of mountain lions and bobcats in the Santa Monica Mountains (including in the SMMNRA) and Simi Hills of Los Angeles and Ventura Counties, Riley et al (2007) found that mountain lions were "less urban-associated than bobcats… but both mountain lions… diagnosed with anticoagulant intoxication died after spending the bulk of their last month in the most developed parts of their home ranges." Additionally, a mountain lion's diet is primarily composed of ungulates (primarily deer), although they will also eat rodents, insects, and smaller predators, depending upon location, season, and abundance (Iriarte et al (1990) and Riley et al (2007)). However, Riley et al (2007) found that "coyotes made up 15% and 7% of the kills for the 2 lions that died of anticoagulant intoxication." This suggests that the mountain lions that died due to anticoagulant toxicity spent more time in the developed part of their home ranges and were consuming more coyotes than the mountain lions that died due to other causes.

Of the 41 bobcats found in five counties and analyzed between 1995 and 2010, approximately 85% tested positive for second generation rodenticides, 76% tested positive for brodifacoum, 63% tested for bromadiolone, and 26% tested positive for difethialone (most of the coyotes tested positive for more than one rodenticide). Between 1995 and 2003, Riley et al (2007) analyzed 35 bobcats in the Santa Monica Mountains (including in the SMMNRA) and Simi Hills of Los Angeles and Ventura Counties. Approximately, 94% tested positive for second generation rodenticides, 82% tested positive for brodifacoum, 71% tested for bromadiolone, and 29% tested positive for difethialone. All nineteen bobcats that died due to severe notoedric mange also tested positive for second generation anticoagulant rodenticides, with brodifacoum ranging from trace to 0.56 ppm. In bobcats with levels of more than 0.05 ppm, the association to mange (and mortality) was “highly significant,” with a p-value < 0.01 (using a Mann-Whitney U test or a Fisher’s Exact test). Bobcats are considered strict carnivores and primarily consume rodents and rabbits, although they will also consume insects, reptile, and larger prey (including deer), depending upon availability, season, and preference (Litvaitis (1981)).

Of the 44 coyotes found in seven counties and analyzed between 1998 and 2010, approximately 75% tested positive for second generation rodenticides, 75% tested positive for brodifacoum, 27% tested for bromadiolone, and 9% tested positive for difethialone. Coyotes found in the SMMNRA (a natural area), in “urban” areas of Los Angeles and Ventura Counties, and unknown areas of Los Angeles and Ventura Counties between 1997 and 2003 were analyzed for rodenticides (Riley, 2012). Out of 25 coyotes, 76% tested positive for brodifacoum, 32% tested positive for bromadiolone, and 16% tested positive for difethialone. There was no statistically significant difference (using Chi-square) between the urban and the natural areas. Tables 12 and 13 summarize the results.

Table 12. Number of coyotes analyzed that had anticoagulant rodenticide residues (including trace residues) by location (land use) within Los Angeles and Ventura Counties from 1997 to 2003 (n=25)[1,2].

Land type/ Population Density	Number of Coyotes	Second Generation Anticoagulant Rodenticide			First Generation Anticoagulant Rodenticide	
		Brodifacoum	Bromadiolone	Difethialone	Chlorophacinone	Diphacinone
Urban	14	11 (78.6%)	6 (42.9%)	4 (28.6%)	1 (7.1%)	2 (14.3%)
Unknown	5	4 (80%)	1 (20%)	0 (0%)	0 (0%)	0 (0%)
SMMNRA (Natural Area)	6	4 (66.7%)	1 (16.7%)	0 (0%)	0 (0%)	2 (33.3%)
Total	25	19 (76%)	8 (32%)	4 (16%)	1 (4%)	4 (16%)

1. Samples may be positive for more than one rodenticide.
2. None of the samples were positive for warfarin.

DPR analyzed the coyotes from Los Angeles and Ventura Counties, Lima and Salmon’s raptor study, and the San Joaquin kit fox study, as a group so that the results could be compared. DPR analyzed the animals by location (using land use and/or population density) for rodenticides. See Table 13, below.

Table 13. Number of animal analyzed that had anticoagulant rodenticide residues (including trace residues) by land use and/or population density from 1997 to 2011 (n=209)[1,2].

Land type/Population Density	Number	Second Generation Anticoagulant Rodenticides			First Generation Anticoagulant Rodenticides	
		Brodifacoum	Bromadiolone	Difethialone	Chlorophacinone	Diphacinone
Urban[5]	116	96 (82.8%)[4a]	46 (39.7%)[4a]	7 (6.0%)[4a]	8 (6.9%)	4 (3.4%)
Unknown[6]	16	11 (6.9%)	9 (56.3%)	2 (12.5%)	1 (6.3%)	0 (0%)
Other[7]	20	6 (30.0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Rural[8]	35	33 (94.3%)[4a]	13 (37.1%)[4a]	5 (14.3%)[4a+]	0 (0%)	0 (0%)
Natural[9]	23	6 (26.1%)[4b]	2 (8.6%)[4b+]	0 (0%)[4b+]	1 (4.3%)	3 (13.0%)
Total of these animals[3]	248	152 (61.3%)	70 (28.2%)	14 (5.6%)	10 (4.0%)	7 (2.8%)
Average of the evaluated data[3]	492	339 (68.9%)	183 (37.2%)	41 (8.3%)	18 (3.7%)	53 (10.8%)

1. Animals may be positive for more than one rodenticide. No animal was positive for warfarin.
2. Using a Chi-square test (with a Yates correction for continuity when appropriate (i.e., at least 20% of the cells had a frequency of less than 5 (per (a) Preacher (2001), (b) calculation, and/or (c) both))), the three second generation anticoagulant rodenticides (as a group, using the actual numbers in the table (i.e., not the percentages)) were analyzed at each land use type/the animal's location. When the notations are the same (eg, 2a and 2a) the locations did not differ statically significantly ($p>0.05$) from each other (Preacher (2001)). When they differ (eg, 2a and 2b), they are statically significantly different ($p<0.05$) from each other.
3. "Average data" is the cumulative data (from Tables 2 and 7) and is there for comparison to the total data.
4. Using a Chi-square test (with a Yates correction for continuity when appropriate, Preacher (2001)), the three second generation anticoagulant rodenticides (individually, using the actual numbers in the table (i.e., not the percentages)). When the notations are the same (4a-4b), the locations did not differ statically significantly ($p<0.05$) from each other. When they differ, they are statically significantly different ($p<0.05$) from each other. + indicates that because the number was so low, Yates was may have been used and/or it might have been inappropriate to utilize Chi-square.
5. The urban animals include: 1 badger, 1 skunk, 2 Cooper's Hawks, 2 Red-tailed Hawks, 2 Sharp-shinned Hawks, 4 Red-shouldered Hawks, 4 red foxes, 7 Barn Owls, 24 coyotes, and 69 San Joaquin kit foxes.
6. The animals from Unknown areas include: 1 Great Horned Owl, 5 coyotes, and 10 San Joaquin kit foxes.
7. The animals from Other areas include: 1 bobcat, 1 skunk, and 18 San Joaquin kit fox. Other Locations were designated by the study authors and include areas in Kern, San Benito, San Luis Obispo, and Tulare counties and could include urban, suburban, rural, agricultural, and/or natural areas.
8. The animals from Rural areas include: 1 American kestrel, 1 hawk, 2 Great Horned owls, 2 Sharp-shinned hawks, 4 Red-tailed hawks, 7 Red-shouldered hawks, 8 Cooper's hawks, and 10 Barn owls.
9. The animals from Natural areas include: 1 black bear, 9 coyotes, and 13 San Joaquin kit fox.

Even though Table 13 only utilizes subset of the data, and does not include most of the bobcats, mountain lions, foxes, coyotes, or the raptors from the CDFG data, it does include the bobcats and mountain lions from Riley et al (2007), the raptors from Lima and Salmon (2010 and 2012), the coyotes from Riley (2012), and the San Joaquin kit fox study from CDFG (2011 and 2012b). The data also show a statistical difference between the percent of animals with brodifacoum and bromadiolone in the rural and urban environments compared to the natural environment. However, it shows that there is no significant difference in the occurrence of difethialone in rural and urban even though the rodenticide occurred less frequently in natural areas.

Rodenticide Sales/Use Rates

Two DPR databases were used to determine rodenticide use rates in California: Pesticide Use Report (PUR) and "Report of Pesticide Mill Assessments in California" (also referred to as the Mill Assessment Database). All agricultural pesticide use must be reported monthly to County Agricultural Commissioners, who in turn, report the data to DPR. The PUR is a yearly compilation of this data, (reported in total pounds of active ingredient (a.i.)). In California, the term "agricultural use" includes pesticide applications to crops, parks, golf courses, pastures, landscape maintenance, and roadsides/right of ways. Although not considered "agricultural use," all applications made by licensed applicators, including structural application, public health application, and home and garden applications, are included in the PUR database. The PUR does not include applications of pesticides by homeowners or other non-licensed persons, including home and garden use, most industrial uses, and most institutional uses. The Mill Assessment Database indicates pesticide sales (in dollars) and quantity (in pounds or gallons) of all registered pesticides sold in California.

Table 14 compares the average total pounds of first and second generation anticoagulant rodenticide active ingredients sold per year between 2006 and 2010 in California, to the average total pounds of reported use of the same active ingredients for the same years. DPR then subtracted the average annual pounds sold by the average annual pounds reported used to estimate the average annual pounds of rodenticides used by non-licensed persons. For purposes of this analysis, DPR assumed a zero percent error between sales and unlicensed use of anticoagulant rodenticides. However, sales and use are not directly related to each other as a person may buy rodenticide one year, but not necessarily use the rodenticide that year or at all.

Table 14. A comparison of the average per year (2006 to 2010) of rodenticides sold (in pounds a.i.) to the average per year (2006 to 2010) of pounds of rodenticides reported used (PUR) (in pounds a.i.) to an estimated pounds of use of rodenticides by non-licensed personnel (calculated by subtracting the PUR from the total sold).

Type of Rodenticide	Rodenticide	Total Sold[1] (lbs. of a.i. (%))	PUR[2] (lbs. of a.i. (%))	Estimated Non-licensed Use[3] (lbs. of a.i. (%))
Second Generation Anticoagulant Rodenticides	Brodifacoum	26.58 (6.54%)	3.07 (2.66%)	23.51 (8.09%)
	Bromadiolone	51.02 (12.56%)	32.48 (28.10%)	18.54 (6.38%)
	Difencoum[4]	0.25 (0.06%)	0.015 (0.01%)	0.235 (0.08%)
	Difethialone	4.49 (1.1%)	3.64 (3.15%)	0.85 (0.29%)
First Generation Anticoagulant Rodenticides	Chlorophacinone	66.54 (16.38%)	17.42 (15.07%)	49.12 (16.79%)
	Diphacinone	226.99 (55.9%)	56.70 (49.05%)	170.29 (58.57%)
	Warfarin	30.44 (7.49%)	2.27 (1.96%)	28.17 (9.69%)
Total Rodenticides		406.32 (100.00%)	115.595 (100.00%)	270.485 (100.00%)

1. From the Mill Assessment Database.
2. From the PUR database. The PUR includes pesticide applications on parks, golf courses, pastures, structural pest control, landscape maintenance, roadsides/right of ways, and crops, and all pesticide applications made by licensed applicators.
3. Calculated by subtracting the "PUR" Use from the Total Sold. Estimates the rodenticides applied by non-licensed applicators (i.e., homeowners, building and maintenance workers, custodians).
4. Two (2) year (2009 and 2010) average.

If the pounds of anticoagulant rodenticides sold or reported used in California per year seem low, please note that the figures are in pounds of "active ingredient," not pounds of product containing the active ingredient. Most anticoagulant rodenticides contain around 0.002% to 0.005% active ingredient. Therefore, over 200,000 pounds of formulated product containing the active ingredient brodifacoum were sold or used in California per year.

When reporting pesticide use to DPR, applicators must indicate a "use site." Table 15 demonstrates how much (both in pounds of a.i. and percent) of the reported use of each anticoagulant rodenticide, between 2006 and 2010, was identified as used on a "Public Health," "Regulatory Pest Control," "Structural Pest Control," or "Vertebrate Pest Control" use site.

Table 15. Reported annual use for Public Health, Regulatory Pest Control, Structural Pest Control and Vertebrate Pest Control separated out in pounds of active ingredient (lb of a.i.) and percentage that each use represents of the a.i. for each rodenticide of the seven anticoagulant rodenticides between 2006 and 2010.

Type of Rodenticide	Rodenticide	Total PUR[1] (lbs. of a.i.)	Public health (lbs. of a.i.) (% of use)	Regulatory pest control (lbs. of a.i.) (% of use)	Structural pest control (lbs. of a.i.) (% of use)	Vertebrate pest control (lbs. of a.i.) (% of use)	Other Uses (lbs. of a.i.) (% of use)
Second Generation Anticoagulant Rodenticides	Brodifacoum	3.07	0.004 (0.12%)	0.01 (0.32%)	2.62 (85.45%)	0.10 (3.10%)	0.336 (10.94%)
	Bromadiolone	32.48	0.61 (1.86%)	0.003 (0.01%)	28.11 (86.54%)	0.48 (1.49%)	3.277 (10.09%)
	Difenacoum[2]	0.015	0 (0.00%)	0.001 (6.67%)	0.008 (53.33%)	0.001 (6.67%)	0.005 (33.33%)
	Difethialone[3]	3.64	0 (0.00%)	0 (0.00%)	2.08 (57.20%)	0.01 (0.36%)	1.55 (42.58%)
First Generation Anticoagulant Rodenticides	Chlorophacinone	17.42	0 (0.00%)	0 (0.00%)	1.50 (8.58%)	2.18 (12.54%)	13.74 (78.87%)
	Diphacinone	56.70	0.19 (0.34%)	2.53 (4.47%)	39.19 (69.12%)	10.38 (18.30%)	4.13 (7.28%)
	Warfarin	2.27	0.003 (0.12%)	0 (0.00%)	0.19 (8.50%)	1.70 (74.67%)	0.377 (16.61%)

1. From the PUR database. The PUR includes pesticide applications on parks, golf courses, pastures, structural pest control, landscape maintenance, roadsides/right of ways, and crops and pesticide applications made by licensed applicators.
2. Two (2) year (2009 and 2010) average.
3. In 2010, the PUR for difethialone was likely reported in gallons instead of pounds, so a 4-year average for the Structural Use data was utilized (2006 to 2009).

Between 2006 and 2010, of the four second generation rodenticides, bromadiolone was the highest in terms of average annual total of pounds of active ingredient sold and reported used. Approximately 51 pounds of bromadiolone were reported sold, and approximately 33 pounds were reported used. Of the 33 pounds of bromadiolone reported used, approximately 87% was for structural pest control. DPR estimates that 19 pounds of bromadiolone were used by non-licensed persons.

Brodifacoum was the second highest second generation anticoagulant rodenticide in terms of average annual pounds of active ingredient sold. However, it is third highest in terms of pounds reported used. An average of approximately 27 pounds of brodifacoum active ingredient was sold annually in California over the four years. However, only three pounds of brodifacoum were reported used. Based on the difference between sales and reported use, DPR estimates that 89% of brodifacoum use was by non-licensed persons (homeowners, building and maintenance workers, custodians, etc.).

This information is not surprising as the majority of products containing brodifacoum were marketed for use by homeowners and non-licensed personnel, whereas the structural pest control industry has favored the use of bromadiolone. As shown in Table 14, both chemicals have been used in structural pest control, just by different types of applicators (i.e., licensed vs. unlicensed).

As shown in Table 15, there have been relatively few sales and/or reported use in California of either difethialone or difenacoum. This may be a reflection of the fact that these are the most recent second generation anticoagulant rodenticides to receive registration in California, not that these rodenticides will not cause a problem for non-target wildlife.

Uncertainties

The scope of DPR's analysis is limited to available data. The data show that exposure and toxicity from second generation anticoagulant rodenticides is occurring to non-target wildlife. However, the data do not tie that exposure/toxicity to any particular rodenticide use pattern (e.g., indoor versus outdoor use of rodenticide). As mentioned above, DPR attempted to separate use of second generation anticoagulant rodenticides by licensed (professional) versus unlicensed personnel by subtracting the average pounds reported use from the average annual pounds sold. However, sales and use are not directly related to each other as a person may buy a rodenticide one year, but not necessarily use the rodenticide that year or at all. In addition, it is not known how much of the "estimated use" of second generation anticoagulant rodenticides by unlicensed persons is for industrial, institutional, home/garden, or other uses, and how much is correctly applied, accidently mishandled, or intentionally misused.

Morzillo and Mertig 2011(a) found that only 10% of residents who used rodenticides were aware of the potential non-target effects. Additionally, Morzillo and Schwartz (2011) found that residents attempt to control target animals, as well as non-target pests and non-target carnivores, San Joaquin kit fox, coyotes, and bats, particularly in single-family homes. Bartos et al (2012) found that residents in the San Fernando Valley and Bel Air-Hollywood used rodenticides to target rats and mice, as well as opossums, snakes, and raccoons up to 300 feet from structures (the limit is 100 feet). Only 42% of participants admitted knowing that rodenticides might affect wildlife. PCOs were primarily called about outdoor landscaping and primarily used snap traps to control rats and mice. Of the 7 that responded, 4 used exclusion, 3 used second generation rodenticides, and 2 used first generation anticoagulants.

Additionally, there are known cases of illegal use. In 2010, the Forest Service cleaned up and restored 335 illegal marijuana sites in national forests in California, removing more than 300 pounds of pesticides (Ferrell (2011) and USDA Forest Service (2011)), including rodenticides which are used to protect the marijuana plants from rodents. Ferrell stated that, "anticoagulant rodenticide… contamination could contribute to continued decline of the Fisher's population." Additionally, according to Gurrola (2010), in certain counties, medical marijuana "has had problems with outdoor growers using massive quantities of rodenticides to protect their crops from rodents," which can cause "secondary poisoning to non-target species and… (m)edical marijuana patients."

Summary
The data clearly indicate that exposure and toxicity to non-target wildlife from second generation anticoagulant rodenticides is a statewide problem. Research data from various locations throughout California indicate that exposure is occurring in many taxa and in every ecosystem. Mammals, birds, and even a reptile, have tested positive for second generation rodenticides. Based on the data provided, DPR believes that the exposure of wildlife to second generation rodenticides is a problem in both urban and rural areas. While the data show exposure and that these exposures put San Joaquin kit fox "in danger of extinction," they do not link specific uses, or location of use of second generation anticoagulant rodenticide (i.e., indoors versus outdoors, homeowners versus professionals) that resulted in the exposure.

Additionally, although brodifacoum was found less often in the natural areas, second generation anticoagulant rodenticides were still found in animals in natural areas. The data also indicate that brodifacoum and difethialone are extremely toxic to both birds and mammals. Bromadiolone and difenacoum are moderately toxic to birds, but extremely toxic to mammals.

Brodifacoum was first registered for use in California in 1983. An average of 27 pounds of brodifacoum active ingredient were sold each year for the last five years, 12 pounds of which were reported used by licensed by licensed pest control applicators. While brodifacoum accounts for approximately 7% of all anticoagulant rodenticides sold, residues of brodifacoum were found in approximately 68% of the animals that DPR analyzed, including coyotes, bobcats, mountain lions, endangered San Joaquin kit foxes, and federally protected raptors. Of the animals analyzed between 1995 and 2011, brodifacoum was likely involved in approximately 13% of animal mortalities and was solely responsible for 9% of animal mortalities.

Bromadiolone was first registered in California in 1982. An average of 51 pounds per year of bromadiolone active ingredient was sold in California between 2006 and 2010, approximately 63% of which was reported used by licensed pest control applicators. Of the rodenticides sold in California, bromadiolone accounted for approximately 13% of anticoagulant rodenticide use. Bromadiolone residues were found in approximately 36% of the animals analyzed, including coyotes, bobcats, mountain lions, endangered San Joaquin kit foxes, and federally protected raptors. Between 1995 and 2011, bromadiolone was likely involved in approximately 3% of animal mortalities.

Difethialone was first registered for use in California in 1997. Difethialone accounts for approximately 1% of anticoagulant rodenticide sales, with approximately 80% reported used by licensed pest control applicators. Residues were found in approximately 8% of the animals analyzed, including bobcats, mountain lions, coyotes, and federally protected raptors. While DPR has no data indicating that difethialone was directly involved in an animal mortality, the data do indicate that the percent of animals with difethialone residues above the most sensitive LD_{50} is relatively high compared to the percent of difethialone sold. Based on its half-life and toxicity data, difethialone appears to be most similar to brodifacoum.

Difenacoum, the newest second generation anticoagulant rodenticide, was first registered with the DPR in 2008. Between 2009 and 2010, difenacoum accounted for approximately 0.3% of the anticoagulant rodenticide that was sold, almost all of which was sold for unlicensed use. In England, between 1998 and 2006, there were eight to 36 “wildlife incidents” per year involving difenacoum. The affected animals included raptors, song birds (i.e., passerines), game birds, domestic animals (dogs and cats), wild canids, and rodents (U.S. EPA, 2007). Based on its half-life and toxicity data, difenacoum appears to be most similar to bromadiolone.

The data also show that exposure of wildlife to second generation anticoagulant rodenticides can lead to sub-lethal effects. Multiple studies have shown that sub-lethal doses can cause lethargy, shortness of breath, anorexia, bloody diarrhea, and tenderness of the joints. Riley et al’s (2007) study of bobcats is an example of sub-lethal effects. Mortality in bobcats due to notoedric mange had not previously been reported as a significant pathogen in wild felid; mange has been strongly correlated to brodifacoum ($p<0.05$), but has not been shown to be caused by rodenticides. This shows that even sub-lethal exposures to anticoagulants may contribute to the ill thrift of the animal and hence the mortality in a wild animal. In addition, to date, very few studies have looked at rodenticide residues in fetuses or in newly whelped or hatched animals. Klein Sereiys’s (2012) data, which found residues in a bobcat fetus, indicate that rodenticides are able to pass the placental barrier. The sub-lethal effects of rodenticides reduce the biological fitness of wildlife.

Conclusion

Based on the data above, DPR finds that use of two of the four second generation anticoagulant rodenticides--brodifacoum and bromadiolone-- present a hazard related to persistent residues in target animals resulting in impacts to non-target wildlife. Because they are similar in half-life and toxicity, DPR also find that if the use of difethialone and difenacoum were to increase, rodenticides containing those two second generation anticoagulant rodenticides may also present a hazard related to persistent residues in target animals.

Bibliography

Albert, C. A., L. K. Wilson, P. Mineau, S. Trudeau, and J. E. Elliott, 2009, "Anticoagulant Rodenticides in Three Owl Species from Western Canada, 1988-2003," *Arch Environ Contam Toxicol*, Vol. 58, No. 2, Pp. 451-459.

Annex I-Norway, 2007, "Directive 98/8/EC Concerning the Placing Biocidal Products on the Market," Assessment report: Difethialone-Product Type 14, <http://ihcp.jrc.ec.europa.eu/our_activities/public-health/risk_assessment_of_Biocides/doc/ANNEX_I/AR/AnnexI_AR_104653-34-1_PT14_en.pdf/view>, accessed on April 19, 2012.

Arndet, Eva, 2012, Urban business attitudes regarding rodents, rodent control methods, and impact on wildlife, An Undergraduate Thesis Submitted to Oregon State University, <http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/35798/ArndtFinal%20thesis%20paper%2006-13-12_FINAL.pdf?sequence=1>, accessed on June 9, 2013.

Bartos, M; Dao, S; Douk, D; Falzone, S; Gumerlock, E; Hoekstra, S; Kelly-Reif, K; Mori, D; Tang, C; Vasquez, C; Ward, J; Young, S; Morzillo, A.; Riley, S: and Longcore, T, 2013, Use of Anticoagulant Rodenticides in Single-Family Neighborhoods Along an Urban-Wildland Interface in California, *Cities and the Environment (CATE)*: Vol. 4: Iss. 1, Article 12. Available at: <http://digitalcommons.lmu.edu/cate/vol4/iss1/12>, accessed on June 9, 2013.

Blakenship, T. L., 1995, "Coyote Interactions with Other Carnivores," in the Symposium Proceedings for "Coyotes in the Southwest: A Compendium of Our Knowledge," <http://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1039&context=coyotesw>, accessed on September 6, 2012.

Bloom, P. H., and S. J. Hawks, "Food Habits of Nesting Golden Eagles in Northeast California and Northwest Nevada," *Raptor Research*, 1982, <http://elibrary.unm.edu/sora/jrr/v016n04/p00110-p00115.pdf>, accessed on September 6, 2012.

Booth, L. H., P. Fisher, V. Heppelthwaite, and C. T. Eason, 2003, "Toxicity and Residues of Brodifacoum in Snails and Earthworms," DOC Science Internal Series 143, Published by the New Zealand Department of Conservation, <http://www.doc.govt.nz/upload/documents/science-and-technical/dsis143.pdf>, accessed on May 14, 2012.

Booth, L. H., C. T. Eason, and E. B. Spurr, "Literature Review of the Acute Toxicity and Persistence of Brodifacoum to Invertebrates," *Science for Conservation*, 2001, <http://www.doc.govt.nz/upload/documents/science-and-technical/Sfc177.pdf>, accessed on May 25, 2012.

Brakes, C. R., and R. H. Smith, "Exposure of Non-Target Small Mammals to Rodenticides: Short-Term Effects, Recovery and Implications for Secondary Poisoning," *Journal of Applied Ecology,* 2005, <http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2005.00997.x/full>, accessed on July 2, 2012.

Buckle, Alan (University of Reading), "Comparative Efficacy of Rodent Control Methods: Impacts of the Risk Mitigation Decision and Draft Notice of Intent to Cancel," presentation to DPR, Sacramento, California, April 3, 2012.

Buckle, Alan (University of Reading), "Status of the Review of Rodenticides by the European Commission and EU Member States," presentation to DPR, Sacramento, California, April 3, 2012.

California Department of Fish and Game (CDFG), 1999, Table: California Wildlife Submitted for Anticoagulant Residue Analysis between 1994-1999.

Carrete, M., J. A. Sanchez-Zapata, and J. F. Calvo, "Breeding Densities and Habitat Attributes of Golden Eagles in Southeastern Spain," *Journal of Raptor Research*, 2000, <http://elibrary.unm.edu/sora/jrr/v034n01/p00048-p00052.pdf>, accessed on September 6, 2012.

CDFG, 2000, Table: California Wildlife Submitted for Anticoagulant Residue Analysis between 1994-2000.

CDFG, 2003, Table: California Wildlife Submitted for Anticoagulant Residue Analysis between 1994-2003.

CDFG, 2010, "A Status Review of the Fisher *(Martes pennanti)* in California," February 2010, <http://www.dfg.ca.gov/wildlife/nongame/publications/docs/FisherStatusReviewComplete.pdf>, accessed on April 19, 2012.

CDFG, 2011, "Anticoagulant Rodenticide Exposure in an Urban Population of the San Joaquin Kit Fox *Vulpes macrotis multicar,*" unpublished report.

CDFG, 2012a, Excel database provided to DPR.

CDFG, 2012b, Excel database of San Joaquin Kit Fox data provided to DPR.

Center for Disease Control (CDC), 2010, "Rodents," last updated 2010, <http://www.cdc.gov/rodents/>, accessed April 20, 2012.

CDC, 2011a, “California Compendium of Plague Control,” last updated 2011, <http://www.cdph.ca.gov/HealthInfo/discond/Documents/2011CAPlagueCompendium.pdf>, accessed on April 19, 2012.

CDC, 2011b, “Diseases Directly Transmitted by Rodents,” last updated June 2011, <http://www.cdc.gov/rodents/diseases/direct.html>, accessed on April 19, 2012.

CDC, 2012a, “Diseases Indirectly Transmitted by Rodents,” last updated January 2012, <http://www.cdc.gov/rodents/diseases/indirect.html>, accessed on April 19, 2012.

CDC, 2012b, “Controlling Rodents,” last updated April 19, 2012, <http://www.epa.gov/opp00001/controlling/rodents.htm#Treating>, accessed on April 19, 2012.

Collins, P. W., and B. C. Latta, “Nesting Season Diet of Golden Eagles on Santa Cruz and Santa Rosa Islands Santa Barbara County, California,” Santa Barbara Museum of Natural History Technical Reports – Number 3, <http://www2.ucsc.edu/scpbrg/PDFFiles/Collins_Latta_GOEA_FinalReport.pdf>, accessed on September 6, 2012.

Craddock, P., 2003, “Aspects of the Ecology of Forest Invertebrates and the Use of Brodifacoum,” Unpublished PhD thesis, The University of Auckland, New Zealand, <https://researchspace.auckland.ac.nz/handle/2292/316>, accessed on May 25, 2012.

Cox, P. and R.H. Smith, 1992, “Rodenticide ecotoxicology: pre-lethal effects of anticoagulants on rat behavior,” Proc. Vertebr. Pest Conf, 15:165-170.

Cypher, B. 2012. LA Times on February 19, 2012. <http://articles.latimes.com/2012/feb/19/local/lame-kit-fox-20120220>, accessed June 5, 2013.

Department of Environmental Conservation, 2012, “Wildlife Necropsy Reports: Diagnosing Causes of Fatalities in Wild Animals,” <http://www.dec.ny.gov/animals/81470.html>, accessed on April 19, 2012.

Dowding, J. E., E. C. Murphy, and C. R. Veitch, 1999, “Brodifacoum Residues in Target and Non-Target Species Following an Aerial Poisoning Operation on Motuihe Island, Hauraki Gulf, New Zealand,” *New Zealand Journal of Ecology*, Vol. 23, No. 2, Pp. 207-214.

Eason, C. T., K. A. Fagerstone, J. D. Eisemann, S. Humphrys, J. R. O’Hare, and S. J. Lapidge, 2010, “A Review of Existing and Potential New World and Australasian Vertebrate Pesticides with a Rationale for Linking Use Patterns to Registration Requirements,” *USDA National Wildlife Research Center – Staff Publications,* Paper 903, <http://digitalcommons.unl.edu/icwdm_usdanwrc/903>, accessed on April 19, 2012.

Eason, C. T., L. Milne, M. Potts, G. Morriss, G. R. G. Wright, and O. R. W. Sutherland, "Secondary and Tertiary Poisoning Risks Associated with Brodifacoum," *New Zealand Journal of Ecology*, 1999, <http://www.nzes.org.nz/nzje/free_issues/NZJEcol23_2_219.pdf>, accessed on May 14, 2012.

Eason, C. T., and S. Ogilvie, 2009, "A Re-Evaluation of Potential Rodenticides for Aerial Control of Rodents," Research & Development Series 312, New Zealand Department of Conservation, Wellington.

Eason, C. T., and E. B. Spurr, "Review of the Toxicity and Impacts of Brodifacoum on Non-Target Wildlife in New Zealand," *New Zealand Journal of Zoology*, 1995, <http://dx.doi.org/10.1080/03014223.1995.9518055>, accessed on May 14, 2012

Eason, C. T., and M. Wickerstrom, 2001, "Vertebrate Pesticide Toxicology Manual (Poisons): Information on Poisons Used in New Zealand as Vertebrate Pesticides," New Zealand Department of Conservation, <http://www.doc.govt.nz/upload/documents/science-and-technical/docts23.pdf>, accessed on May 14, 2012.

Eason, C. T., G. R. Wright, and D. Batcheler, "Anticoagulant Effects and the Persistence of Brodifacoum in Possums *(Trichosurus vulpecula)*," *New Zealand Journal of Agricultural Research*, 1996, <http://www.tandfonline.com/doi/pdf/10.1080/00288233.1996.9513199>, accessed on May 14, 2012.

Erickson, W., and D. Urban, 2004, "Potential Risks of Nine Rodenticides to Birds and Nontarget Mammals: a Comparative Approach," Pp. 15-25, EPA-HQ-OPP-2004-0033-0003, United States Environmental Protection Agency (U.S. EPA), Washington, D.C.

Fairbrother, Anne, Susan Kane Driscoll, and Richard Stroud (Exponent), "Risks of Rodenticides to Nontarget Wildlife: Comments on EPA's Risk Assessment and Mitigation Options," presentation to DPR, Sacramento, California, April 3, 2012.

Ferrell, D, 2011, "Exploring the Problem of Domestic Marijuana Cultivation" in a Statement to the United States Senate Caucus on International Narcotics Control, on November 7, 2011, <http://drugcaucus.senate.gov/hearing-12-7-11/Ferrell-Testimony.pdf>, accessed on September 4, 2012.

Fisher, P. M., "Residual Concentrations and Persistence of the Anticoagulant Rodenticides Brodifacoum and Diphacinone in Fauna," doctoral dissertation, Lincoln University, Lincoln, New Zealand, 2009, <http://researcharchive.lincoln.ac.nz/dspace/bitstream/10182/930/3/Fisher_PhD.pdf>, accessed on April 19, 2012.

Fisher, P., R. Griffiths, C. Speedy, and K. Broome, 2011, “Environmental Monitoring for Brodifacoum Residues after Application of Baits for Rodents Eradication,” In: Veitch, C. R., M. N. Clout, and D. R. Towns, (eds.), 2011, “Island Invasives: Eradication and Management,” IUCN, Gland, Switzerland, Pp. 300-304, <http://www.issg.org/pdf/publications/Island_Invasives/pdfHQprint/3FisherP.pdf>, accessed on May 14, 2012.

Fisher, P., C. O’Connor, G. Wright, and C. T. Eason, 2003, “Persistence of Four Anticoagulant Rodenticides in the Livers of Laboratory Rats,” DOC Science Internal Series 139, New Zealand Department of Conservation, <http://www.conservation.org.nz/upload/documents/science-and-technical/dsis139.pdf>, accessed on April 19, 2012.

Fisher, P., and A. Saunders, 2012, “Case Study: Brodifacoum Rodenticide-Assessing Non-Target Risk of Galapagos Tortoises and Other Reptiles,” <http://www.isinz.com/documents/Brodifacoum_Galapagos_11_11.pdf>, accessed on April 19, 2012.

Frost, N., “San Joaquin Kit Fox Home Range, Habitat Use, And Movements in Urban Bakersfield,” master’s thesis, Humboldt State University, Humboldt, California, 2005, <http://humboldt-dspace.calstate.edu/bitstream/handle/2148/36/Frost.pdf?sequence=1>, accessed on September 6, 2012.

Gabriel, M. W., 2011, “Update on Exposure to Anticoagulant Rodenticides in Fishers,” Presented July 19, 2011 at the Sierra Nevada Adaptive Management Project (SNAMP), <http://snamp.cnr.berkeley.edu/static/documents/2011/07/22/Jul-14-2011_FisherIT_MouradGabriel.pdf>, accessed on April 19, 2012.

Gabriel, M. W., L. Woods, D. Clifford, S. McMillin, and R. Poppenga, 2012, “Frequently Asked Questions about Rodenticide Baits - Q & A: Fishers & Rodenticide Exposure,” <http://www.iercecology.org/wp-content/uploads/2012/05/Fisher-AR-QA-final-Product.pdf>, accessed on May 14, 2012.

Gabriel, M. W., L Woods, R Poppenga, R. A. Sweitzer, C. Thompson, S. M. Matthews, M. Higley, S. M. Keller, K. Purcell, R. H. Barrett, G. M. Wengert, B. N. Sacks, and D. L. Clifford, 2012a, “Anticoagulant Rodenticides on our Public and Community Lands: Spatial Distribution of Exposure and Poisoning of a Rare Forest Carnivore,” *PLOS One*, <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0040163>, accessed on July 14, 2012.

Gatto, A. E., T. G. Grubb, and C. L. Chambers, "Red-tailed Hawk Dietary Overlap with Northern Goshawks on the Kaibab Plateau, Arizona," *Journal of Raptor Research*, 2005, <http://www.rmrs.nau.edu/publications/GattoEtal/GattoEtal.pdf>, accessed on September 7, 2012.

Goodrich, J. J., "Stopover Ecology of Autumn-Migrating Raptors in the Central Appalachians," doctoral dissertation, Pennsylvania State University, University Park, Pennsylvania, 2010, <http://www.globalraptors.org/grin/researchers/uploads/409/goodrich_dissertation_2010.pdf>, accessed on September 7, 2012.

Guinn, J. E., "Bald Eagle Nest Site Selection and Productivity Related to Habitat and Human Presence in Minnesota," doctoral dissertation, North Dakota State University, Fargo, North Dakota, 2004, <http://files.dnr.state.mn.us/eco/nongame/projects/consgrant_reports/2004/2004_guinn.pdf>, accessed on September 7, 2012.

Gurrola, R., 2010, "White Paper on Medical Marijuana," Tehama County White Paper on Medical Marijuana, <http://www.counties.org/images/users/1/Med%20marijuana%20WP%20Tehama.pdf>, accessed on April 19, 2012.

Harper, G. A., Zabala, J., and Carrion, V., 2011, "Monitoring of a Population of Galápagos Land Iguanas (*Colonophus subcristatus*) during a Rat Eradication Using Brodifacoum," In: Veitch, C. R., Clout, M. N. and Towns, D. R. (eds.), *Island Invasives: Eradication and Management*, Pp. 309-312, IUCN, Gland, Switzerland, <http://www.issg.org/pdf/publications/Island_Invasives/pdfHQprint/3HarperIguanas.pdf>, accessed on April 19, 2012.

Hiraldo, F., M. Delibes, and J. Bustamonte, and R. R. Estrella, "Overlap in the Diets of Diurnal Raptors Breeding at the Michilía Biosphere Reserve, Durango, Mexico," *Journal of Raptor Research*, 1991a, <http://www.ebd.csic.es/bustamante/publicaciones/Hiraldo_et_al_%281991%29_J_Raptor_Res_25_25-29.PDF>, accessed on September 7, 2012.

Hiraldo, F., M. Delibes, and J. A. Donazar, "Comparison of Diets of Turkey Vultures in Three Regions of Northern Mexico," *Journal of Field Ornithology*, 1991b, <http://elibrary.unm.edu/sora/JFO/v062n03/p0319-p0324.pdf>, accessed on September 7, 2012.

Hoare, J. M., and K. M Hare, "The Impact of Brodifacoum on Non-Target Wildlife: Gaps in Knowledge," *New Zealand Journal of Ecology*, 2006, <http://www.nzes.org.nz/nzje/free_issues/NZJEcol30_2_157.pdf>, accessed on May 14, 2012.

Hodeenbach, G., J. Johnson, and C. DiSalvo, 2005, “Mechanical Rodent-Proofing Techniques: A Training Guide for National Park Employees,” National Park Service, <http://nmhealth.org/pdf/NPS_RP_Manual_v2.pdf>, accessed on July 2, 2012.

Housenger, J., and J. L. Melendez, 2011, “Risks of Difethialone Use to the Federally Threatened Alameda Whipsnake (*Masticophis Lateralis euryxanthus*), and the Federally Endangered Salt March Harvest Mouse (*Reithrodontomys raviventris*) and San Joaquin Kit Fox (*Vulpes macrotis mutica*),” Environmental Fate and Effects Division, Office of Pesticide Programs, Washington, D.C., <http://www.epa.gov/espp/litstatus/effects/redleg-frog/2011/difethialone/assessment.pdf>, accessed on July 2, 2012.

Housenger, J., and J. L. Melendez, 2012, “Risks of Brodifacoum Use to the Federally Threatened Alameda Whipsnake (*Masticophis Lateralis euryxanthus*), and the Federally Endangered Salt March Harvest Mouse (*Reithrodontomys raviventris*) and San Joaquin Kit Fox (*Vulpes macrotis mutica*),” Environmental Fate and Effects Division, Office of Pesticide Programs, Washington, D.C., <http://www.epa.gov/espp/litstatus/effects/redleg-frog/2012/brodifacoum/analysis.pdf>, accessed on July 2, 2012.

Howald, G. R., “The Risk of Non-Target Species from Brodifacoum Used to Eradicate Rats from Langara Island, British Columbia, Canada,” master’s thesis, University of British Columbia, Vancouver, BC, Canada, 1997, <https://circle.ubc.ca/bitstream/handle/2429/6509/ubc_1997-0545.pdf?sequence=1>, accessed on May 14, 2012.

Howald, G., K. R. Faulkner, B. Tershy, B. Keitt, H. Gellerman, E. Creel, M. Grinnell, S. T. Ortega, and D. A. Croll, “Eradication of Black Rats From Anacapa Island: Biological and Social Considerations,” Fauna and Flora International, *Oryx*, 2009, <http://bio.research.ucsc.edu/people/croll/pdf/Howald_2005.pdf>, accessed on April 19, 2012.

IPCS (International Programme on Chemical Safety), 2010, “Data Sheet on Pesticides No. 57: Brodifacoum,” <http://www.inchem.org/documents/pds/pds/pest57_e.htm>, accessed on June 4, 2012.

Iriarte, J. A., W. L. Franklin, W. E. Johnson, and K. H. Redford, 1990, “Biogeographic Variation of Foods Habits and Body Size of the America Puma,” *Oecologia*, Vol. 85, No. 2, Pp. 185-190.

Jacobs, J. P., and E. A. Jacobs, 2002, “Conservation Assessment for Red-Shouldered Hawk *(Buteo lineatus)* National Forests of North Central States” for the USDA Forest Service Eastern Region, <http://www.fs.fed.us/r9/wildlife/tes/ca-overview/docs/red_shouldered_hawk_ca_1202final.pdf>, accessed on September 6, 2012.

Kasparian, M. A., E. C. Hellgren, and S. M. Ginger, "Food Habits of the Virginia Opossum during Raccoon Removal in the Cross Timbers Ecoregion, Oklahoma," *Oklahoma Academy of Science,* 2002, <http://digital.library.okstate.edu/oas/oas_pdf/v82/p73_78.pdf>, accessed on September 7, 2012.

Kay, J., 2007a, "Groups Debate Poison Use after 3 Hawks Die, 1 Survives," *San Francisco Chronicle, SFGate,* <http://www.sfgate.com/cgi-bin/article.cgi?f=/c/a/2007/03/16/BAGSFOME621.DTL>, accessed on May 22, 2012.

Kay, J., 2007b, "Rat Poison Use Discontinued in Golden Gate Park," *Scrippsnews*, <http://www.scrippsnews.com/node/20351>, accessed on May 22, 2012.

Klein Serieys, L., 2012, Data provided to DPR.

Koprowski, J. L., 1994, "Sciurus niger," in Mammalian Species, No. 479, <http://www.science.smith.edu/msi/>, accessed on September 7, 2012.

Lambert, O, H. Pouliquen, M. Larhantec, C. Thorin, and M. L'Hostis, "Exposure of Raptors and Waterbirds to Anticoagulant Rodenticides (Difenacoum, Bromadiolone, Coumatetralyl, Coumafen, Brodifacoum): Epidemiological Survey in Loire Atlantique (France)," *Bulletin Environmental Contamination and Toxicology*, 2007, <http://www.researchgate.net/publication/6344862_Exposure_of_raptors_and_waterbirds_to_anticoagulant_rodenticides_(difenacoum_bromadiolone_coumatetralyl_coumafen_brodifacoum)_epidemiological_survey_in_Loire_Atlantique_(France)>, accessed on April 19, 2012.

Larivière, S., and M. Pasitschniak-Arts, 1996, "Vulpes vulpes," in Mammalian Species No. 537, <http://www.science.smith.edu/msi/>, accessed on September 7, 2012.

Lee, J. C., D. A. Osborne, and K. V. Miller, "Foods Eaten by a High-Density Population of Southern Fox Squirrels," *Florida Field Naturalist*, 2001, <http://www.fosbirds.org/sites/default/files/FFNs/FFNv29n1p29-32David.pdf>, accessed on September 7, 2012.

Lima, L. L., and T. P. Salmon, 2010, "Assessing Some Potential Environmental Impacts from Agricultural Anticoagulant Uses," Proceedings of the Twenty-Fourth Vertebrate Pest Conference, Published at University of California, Davis, Pp. 199-203.

Lima, L. L., and T. P. Salmon, 2012, Data used to publish their paper.

Littin, K. E., C. E. O'Connor, and C. T. Eason, "Comparative Effects of Brodifacoum on Rats and Possums," *New Zealand Plant Protection Society*, 2000, <http://www.nzpps.org/journal/53/nzpp_533100.pdf>, accessed on May 25, 2012.

Litvaitis, J. A., 1981, "A Comparison of Coyotes and Bobcat Food Habits in the Wichita Mountains, Oklahoma," Proceedings of Oklahoma Academy of Science, <http://digital.library.okstate.edu/oas/oas_pdf/v61/p81_82.pdf>, accessed on September 4, 2012.

Marrow, C., 2001, "Cholecalciferol Poisoning," Veterinary Medicine Publishing Group, <www.aspcapro.org/mydocuments/n-toxbrief_1201.pdf>, accessed on April 19, 2012.

Marzluff, J. M., S. T. Knick, M. S. Vekasy, L. S. Schueck, and T. J. Zarriello, "Spatial Use and Habitat Selection of Golden Eagles in Southwestern Idaho," *The Auk*, 1997, <http://elibrary.unm.edu/sora/Auk/v114n04/p0673-p0687.pdf>, accessed on September 7, 2012.

Marti, C. D., and M. N. Kochert, "Diet and Trophic Characteristics of Great Horned Owls in Soutwestern Idaho," *Journal of Field Ornithology*, 1996, <http://elibrary.unm.edu/sora/JFO/v067n04/p0499-p0506.pdf>, accessed on September 6, 2012.

McGrew, J., 1979, "Vulpes macrotis," in Mammalian Species No. 123, <http://www.science.smith.edu/msi/pdf/i0076-3519-123-01-0001.pdf>, accessed on September 6, 2012.

McManus, J. J., 1974, "Didelphis virginiana," in Mammalian Species No. 40, <http://www.science.smith.edu/msi/>, accessed September 7, 2012.

McMillin, S. C., R. C. Hosea., B. F. Finlayson, B. L. Cypher, and A. Mekebri, 2008, "Anticoagulant Rodenticide Exposure in an Urban Population of the San Joaquin Kit Fox," Proceedings of the Twenty-Third Vertebrate Pest Conference, March 19, 2008, Pp. 163-165.

"Rodenticide Poisoning: Introduction," *The Merck Veterinary Manual,* Merck Sharp & Dohme Corp., a subsidiary of Merck & Co, New Jersey, 2011, <http://www.merckvetmanual.com/mvm/index.jsp?cfile=htm/bc/213000.htm>, accessed on May 22, 2012.

Miller, L., 2012, "Rodenticide Usage at LVMWD Facilities," e-mail message, April 6, 2012.

Morzillo, A. T., and A. G. Mertig, 2011a, "Linking Human Behavior to Environmental Effects Using a Case Study of Urban Rodent Control," *International Journal of Environmental Studies*, Vol. 68, No. 1, February 2011, Pp. 107-123.

Morzillo, A. T., and A. G. Mertig, 2011b, "Urban Resident Attitudes toward Rodents, Rodent Control Products, and Environmental Effects," *Urban Ecosystems* Vol. 14, Pp. 243-260.

Morzillo, A. T., A. G. Mertig, J. W. Hollister, N. Garner, and J. Liu, “Socioeconomic Factors Affecting Local Support for Black Bear Recovery Strategies,” *Environmental Management,* 2010, <http://www.springerlink.com/content/k58x3360778245jk/fulltext.pdf>, accessed on April 19, 2012.

Morzillo, A. T., and M. D. Schwartz, “Landscape Characteristics Affect Animal Control by Urban Residents,” *Ecosphere,* 2011, <http://www.esajournals.org/doi/pdf/10.1890/ES11-00120.1>, accessed on April 19, 2012.

Munday, J. S., and L. J. Thompson, “Brodifacoum Toxicosis in Two Neonatal Puppies,” *Vet Pathol,* 2003, <http://vet.sagepub.com/content/40/2/216.full.pdf+html>, accessed on May 25, 2012.

Murray, M., 2011, “Anticoagulant Rodenticide Exposure and Toxicosis in Four Species of Birds of Prey Presented to A Wildlife Clinic in Massachusetts, 2006–2010,” *Journal of Zoo and Wildlife Medicine*, Vol. 42, No. 1, Pp. 88–97.

Naz, S., Rana, S. A., M. Javed., and Khalil-ul-Rehman, “Toxicological Effects of Brodifacoum and Food Energy Inhibitor on Some Physiological Parameters in House Rats (*Rattus rattus*),” *Pakistan Veterinary Journal,* 2011, <http://www.pvj.com.pk/pdf-files/31_3/219-222.pdf>, accessed on April 19, 2012.

Naim, M., H. Mohd Noor, A. Kassim, and J. Abu, “Comparison of the Breeding Performance of the Barn Owl *Tyto alba jacanica* under Chemical and Bio-based Rodenticide Baiting in Immature Oil Palms in Malaysia,” Global Science Books, Dynamic Biochemistry, Process Biotechnology and Molecular Biology, 2011, Pp. 5-11, <http://www.globalsciencebooks.info/JournalsSup/images/Sample/DBPBMB_5(SI2)5-11o.pdf>, accessed on July 2, 2012.

Ogilvie, S. C., R. J. Pierce, G. R. G. Wright, L. H. Booth, and C. T. Eason, “Brodifacoum Residue Analysis in Water, Soil, Invertebrates, and Birds after Rat Eradication on Lady Alice Island,” *New Zealand Journal of Ecology*, 1997, <http://www.nzes.org.nz/nzje/free_issues/NZJEcol21_2_195.pdf>, accessed on July 2, 2012.

Papakosta, M., D. Bakaloudis, K. Kikikidou, C. Vlachos, and E. Chatzinikos, “Dietary Overlap Among Seasons and Habitats of Red Fox and Stone Marten in Central Greece,” *European Journal of Scientific Research*, 2010, <http://www.eurojournals.com/ejsr_45_1_12.pdf>, accessed on September 7, 2012.

Peterson, A., 1986, “Habitat Suitability Index Models: Bald Eagle (Breeding Season),” Biological Report 82 (10.126), Fish and Wildlife Service, U.S. Department of the Interior, <http://www.nwrc.usgs.gov/wdb/pub/hsi/hsi-126.pdf>, accessed on September 7, 2012.

Pezzo, F., and F. Morimando, "Food Habits of the Barn Owl, *Tyto alba*, in a Mediterranean Rural Area: Comparison with the Diet of Two Sympatric Carnivores," *Italian Journal of Zoology*, 1995, <http://www.tandfonline.com/doi/pdf/10.1080/11250009509356091>, accessed on September 7, 2012.

Preacher, K. J., 2001, "Calculation for the Chi-Square Test: An Interactive Calculation Tool for Chi-Square Tests of Goodness of Fit and Independence [Computer software]," <http://www.quantpsy.org/chisq/chisq.htm>, accessed on September 4, 2012.

Quinn, J. H., Y. A. Girard, K. Gilardi, Y. Hernandez, R. Poppenga, B. B. Chomel, J. E. Foley, and C. K. Johnson, 2012, "Pathogen and Rodenticide Exposure in American Badgers (Taxidea taxus) in California," *Journal Wildlife Diseases*, Vol. 48, No. 2, Pp. 467-472.

Rattner, B. A., K. E. Horak, S. E. Warner, D. D. Day, C. U. Meteyer, S. F. Volker, J. D. Eisemann, and J. J. Johnston, "Acute Toxicity, Histopathology, and Coagulopathy in American Kestrels (Falco Sparverius) Following Administration of the Rodenticide Diphacinone," *Environmental Toxicity and Chemistry*, 2011, <http://onlinelibrary.wiley.com/doi/10.1002/etc.490/pdf>, accessed on May 25, 2012.

Rahmy, T. R, "Myocardial Alteration in Animals Intoxiated with an Anticoagulant Rodenticide," *Journal of Egyptian Ger Society of Zoology*, 1993, pp 87-98, accessed 12/31/2012.

Riley, S., 2012, Coyote data provided to DPR.

Riley, S. P. D., C. Bromley, R. H. Poppenga, R. A. Uzal, L. Whited, and R. M. Sauvajot, 2007, "Anticoagulant Exposure and Notoedric Mange in Bobcats and Mountain Lions in Urban Southern California," *Journal of Wildlife Management*, Vol. 71, No. 6, Pp. 1874–1884.

Rocha, R. G., E. Ferreira, Y. L. R. Leite, C. Fonseca, and L. P. Costa, "Small Mammals in the Diet of Barn Owls, *Tyto alba* (Aves: Strigiformes) Along the Mid-Arguaia River in Central Brazil," *Zoologica*, 2011, <http://www.scielo.br/pdf/zool/v28n6/03.pdf>, accessed on September 6, 2012.

Roth, II, T. C., and S. L. Lima, "Hunting Behavior and Diet of Cooper's Hawks: An Urban View of the Small-Bird-In-Winter Paradigm," *The Condor*, 2003, <http://wolfweb.unr.edu/homepage/tcroth/Roth%20and%20Lima%202003%20Condor.pdf>, accessed on September 6, 2012.

Sacks, B. N., Wittmer, H. U., Statham, M. J., "The Native Sacramento Valley Red Fox," Report to the California Department of Fish and Game, May 30, 2010, <http://foxsurvey.ucdavis.edu/documents/30May2010_FinalReport_ForDistribution.pdf>, accessed on September 7, 2012.

Shlosberg, A., and L. Booth, 2001, "Veterinary and Clinical Treatment of Vertebrate Pesticide Poisoning – a Technical Review," Pest Control Research, New Zealand, <http://www.pestcontrolresearch.co.nz/docs-bait/treatmentofpoisoning.pdf>, accessed on May 25, 2012.

Spaulding, S. R., and H. Spannring, "Status of Bromethalin Outside the United States," Proceedings of the Thirteenth Vertebrate Pest Conference, March 1, 1988, Pp. 64-69, <http://digitalcommons.unl.edu/vpcthirteen/14>, accessed on April 19, 2012.

Spurr, E. B., "A Review of the Effects of Pesticides on Lizards," *Conservation Advisory Science Notes No. 33*, Department of Conservation, Wellington, 1993, <http://www.doc.govt.nz/upload/documents/science-and-technical/casn33.pdf>, accessed on May 14, 2012.

Steenhof, K., and M. N. Kochert, "Dietary Responses of Three Raptor Species to Changing Prey Densities in a Natural Environment," *Journal of Animal Ecology*, 1998, <http://fresc.usgs.gov/products/papers/1777_Steenhof.pdf>, accessed on September 7, 2012.

Sternberg, R., R. Miller, and A. Korol, 2011, "Risks of Bromadiolone Use to the Federally Threatened Alameda Whipsnake (*Masticophis Lateralis euryxanthus*), the Federally Endangered Salt March Harvest Mouse (*Reithrodontomys raviventris*), and the Federally Endangered San Joaquin Kit Fox (*Vulpes macrotis mutica*)," Environmental Fate and Effects Division, Office of Pesticide Programs, Washington, D.C., <http://www.epa.gov/espp/litstatus/effects/redleg-frog/2011/bromadiolone/assessment.pdf>, accessed on July 2, 2012.

Stone, W. B., J. C. Okoniewski, and J. R. Stedelin, "Poisoning of Wildlife with Anticoagulant Rodenticides in New York," *Journal of Wildlife Diseases*, 1999, <http://www.jwildlifedis.org/content/35/2/187.full.pdf+html?sid=85f66e59-3841-4ca9-9ad7-0439a0d07a33>, accessed on April 19, 2012.

Timm, R. M., 2011, "Pests of Homes, Structures, People, and Pets: House Mice," October 2011, <http://www.ipm.ucdavis.edu/PMG/PESTNOTES/pn7483.html>, accessed on May 22, 2012.

Timm, R. M., T. P. Salmon, and R. E. Marsh, 2012, "Pests of Homes, Structures, People, and Pets: Rats," September 2011, <http://www.ipm.ucdavis.edu/PMG/PESTNOTES/pn74106.html>, accessed on May 22, 2012.

Townsend, M. G., P. J. Bunyan, E. M. Odam, P. I. Stanley, and H. P. Wardall, 1984, "Assessment of the Secondary Poisoning Hazard of Warfarin to Least Weasels," *Journal of Wildlife Management*, Vol. 48, Pp. 628-632.

Thomas P. J., P. Mineau, R. F. Shore, L. Champoux, P. A. Martin, L. K. Wilson, G. Fitzgerald, and J. E. Elliott, 2011, "Second Generation Anticoagulant Rodenticides in Predatory Birds: Probabilistic Characterization of Toxic Liver Concentrations and Implications for Predatory Bird Populations in Canada," *Environment International*, Vol. 37, No. 5, Pp. 914-920.

USDA Forest Service, 2011, "Nation's Forests are Severely Damaged by Marijuana Grow Sites: US Forest Service Law Enforcement Director Testifies on Environmental Impacts, Safety Concerns," Press Release No. 1152, <http://www.fs.fed.us/news/2011/releases/12/marijuana.shtml>, accessed on May 22, 2012.

U.S. EPA, Code of Federal Regulations, Title 40, Protection of the Environment, Parts 150 to 158, U.S. Superintendent of Documents, Washington, D.C., 2011.

U.S. EPA, "Commensal Rodenticide Products Outdoor 50 Foot Restriction for Professional Use Products (Revised to Include Language for Agricultural Products)," EPA-HQ-OPP-2006-0955-0819, March 14, 2012.

U.S. EPA, 2007, "Pesticide Fact Sheet: Difenacoum," Washington, D.C., <http://www.epa.gov/opprd001/factsheets/difenacoum.pdf>, accessed on April 19, 2012.

U.S. EPA, "Risk Mitigation Decision for Ten Rodenticides," EPA-HQ-OPP-2006-0955-0764, May 28, 2008, revised June 24, 2008.

U.S. EPA, "Rodenticides. Draft Notice of Intent to Cancel and Denial," EPA-HQ-OPP-2011-0178-0017," November 2, 2011.

U.S. Fish and Wildlife Service, 2010, San Joaquin Kit Fox (*Vulpes macrotis mutica*) 5-Year Review: Summary and Evaluation <http://ecos.fws.gov/docs/five_year_review/doc3222.pdf>, accessed on June 7, 2013.

U.S. Fish and Wildlife Service, 2012, "Species Profile: Fisher (Martes pennant)", *Environmental Conservation Online System*, <http://ecos.fws.gov/speciesProfile/profile/speciesProfile.action?spcode=A0HS> accessed on May 25, 2012.

U.S. Fish and Wildlife Service, 2013, Endangered Species Act | Overview <http://www.fws.gov/endangered/laws-policies/>, accessed on June 7, 2013.

Valchev, I., Binev, R., Yardanova, V., and Nikolov, Y., “Anticoagulant Rodenticide Intoxication in Animals - A Review,” *Turk. J. Vet. Anim. Sci.,* 2005, <http://journals.tubitak.gov.tr/veterinary/issues/vet-08-32-4/vet-32-4-1-0607-12.pdf>, accessed on May 25, 2012.

Vandenbroucke V., Bousquet-Melou A., De Backer P., Croubels S., 2008, “Pharmacokinetics of Eight Anticoagulant Rodenticides in Mice after Single Oral Administration,” *J Vet Pharmacol Ther.,* Vol. 31, No. 5, Pp. 437-445.

Wade-Smith, J., and B. J. Verts, 1982, “Mephitis mephitis” in Mammalian Species No. 173, <http://www.science.smith.edu/msi/pdf/i0076-3519-173-01-0001.pdf>, accessed on September 6, 2012.

Wagman, M., and A. Shelby, 2012, “Risks of Difenacoum Use to the Federally Threatened Alameda Whipsnake (*Masticophis Lateralis euryxanthus*), the Federally Endangered Salt March Harvest Mouse (*Reithrodontomys raviventris*), and the Federally Endangered San Joaquin Kit Fox (*Vulpes macrotis mutica*),” Environmental Fate and Effects Division, Office of Pesticides Programs, Washington, D.C., <http://www.epa.gov/espp/litstatus/effects/redleg-frog/2012/difenacoum/analysis.pdf>, accessed on July 2, 2012.

Warrick, G. D., H. O. Clark, P. A. Kelly, D. F. Williams, and B. L. Cypher, 2007, “Use of Agricultural Lands by San Joaquin Kit Foxes,” *Western North American Naturalist*, Vol. 67, No. 2, Pp. 270-277.

Watt, B. E., Proudfoot, A. T., Bradberry, S. M., and Vale, J. A, 2005,“Anticoagulant Rodenticides,” *Toxicol Rev.*, Vol. 24, No. 4, Pp. 259-269.

Whitworth, D. L., H. R. Carter, R. J. Young, J. S. Koepke, F. Gress, and S. Fangman, “Initial Recovery of Xantu’s Murrelers Following Rat Eradication on Anacapa Island, California,” *Marine Ornithology*, 2005, <http://www.mendeley.com/research/initial-recovery-of-xantuss-murrelets-following-rat-eradication-on-anacapa-island-california/#page-1>, accessed on July 2, 2012.

WildCare, 2011, Data provided to DPR.

Wisley, S. M., S. W. Buskirk, G. A. Russell, K. B. Ahbry, and W. I. Zielinski, “Genetic Diversity and Structure of the Fisher (*Martes pennant*) in a Peninsular and Peripheral Metapopulation,” *Journal of Mammology*, 2004, <http://www.fs.fed.us/pnw/pubs/journals/pnw_2004_wisely001.pdf>, accessed on April 19, 2012.

Woody, B, M. Murphy, A. Ray, R. Green, “Coagulaphathic Effects and Therapy of Brodifacoum Toxicosis in Dogs,” Netherlands Small Animal Veterinary Association, 1992, pp 23-28.

APPENDIX I: Non-California Data

DPR also evaluated studies conducted in locations other than California. When the data came from a rodent eradication effort, rodenticide use rates were significantly higher than normal label rates. However, the data are still useful for presenting the potential impacts of rodenticides.

Howald et al (2009) utilized brodifacoum to eradicate black rats (*Rattus rattus*) from the three islets of Anacapa Island. An endemic mouse (the Anacapa deer mouse) and several protected birds also inhabited the island. Even though the organizers employed several measures to reduce mortality of the non-target organisms, at least 94 birds were found dead after the bait application including 6 Burrowing Owls, an American Kestrel, 3 Barn Owls, and multiple thrushes.

The Department of Environmental Conservation (2012) necropsied and ran rodenticide analysis on 4 Red-tailed Hawks found dead in Manhattan, New York. One had residues of difethialone, 2 had residues of difethialone, brodifacoum, and bromadiolone, and 1 had residues of difethialone, brodifacoum, bromadiolone, and diphacinone. Based on necropsies conducted by veterinarians, 3 died due to anticoagulant rodenticide poisoning and 1 died due to “complications due to egg laying (oviductal prolapse), possibly exacerbated by hemorrhaging.” The Department of Environmental Conservation concluded that at least 1 of the Red-tailed Hawks most likely died directly from difethialone toxicity.

Stone et al (1999) documented 52 non-target wild animals that appeared to have died due to anticoagulant rodenticide toxicosis in New York between 1989 and 1997. Brodifacoum was found in over 90% of the animals. Raptors (primarily Great Horned Owls and Red-tailed Hawks) comprised half the cases. Eastern gray squirrels, raccoons, and white-tailed deer were the mammals that were most frequently poisoned.

Murray (2011) analyzed the livers of 4 raptor species presented to a wildlife rehabilitation clinic between April 2006 and March 2010. All either died or were euthanized. Of the 161 birds, 139 (86%) had residues of anticoagulant rodenticides, including 100% of the Great Horned Owls, 89% of the Red-tailed Hawks, 87% of the Eastern Screech Owls, and 75% of the Barred Owls. One-hundred thirty-six animals had residues of brodifacoum, including 99% of the positive birds. One Barred Owl and 1 Red-tailed Hawk were positive for both brodifacoum and difethialone, and 1 Barred Owl was positive for bromadiolone. Rodenticide toxicosis was identified as the cause of death in nine animals (5.6% of the animals), all of which had brodifacoum residues.

Howald (1997) examined the Canadian Wildlife Service’s attempt to eradicate the Norway rat *(Rattus norvegicus)* from Langara and Lucy Islands using brodifacoum in baiting stations. Of the radio-collared Norway rats between 13.4% and 33.3% died above ground and some appeared to have been scavenged. Thirteen (100%) ravens tested positive for brodifacoum (with a liver brodifacoum range of 0.985 to 2.522 ppm). The cause of death was confirmed at necropsy and none of the birds were in poor body condition or had any evidence of other diseases. Crows tested positive for brodifacoum up to nine months after the baiting ceased and bald eagles were also confirmed to be exposed. Crows and ravens were observed eating rats and the bait. Snails, slugs, blowfly larva, and other species also tested positive for brodifacoum.

Several papers have suggested that invertebrates might be potential sources of rodenticides to animals that predate invertebrates (Booth et al (2001), Booth et al (2003), Brakes and Smith (2005), Craddock (2003), Fisher et al (2011), Ogilvie et al (1997), and Shlosberg and Booth (2001)). Weta, cockroachs, beetles (*Holcaspis stewartensis* and *Mecodema*), locuses, and land crabs all tested positive for brodifacoum (range: 0.02 to 7.47 ug/g), after either directly consuming or being gavaged with brodifacoum. While the animals themselves appeared relatively insensitive to brodifacoum (with no mortality reported), these animals can travel up to 10 meters and it could take more than ten weeks for the brodifacoum to return to pre-baiting levels. Additionally, brodifacoum caused mortality in three species of snails (*Pachnodus silhouettanus*, *Achatina fulica,* and *Pachystyla bicolor*).

Albert et al (2009) collected 164 dead owls (Barn, Barred, and Great Horned Owls) in Canada. Albert et al conducted necropsies and analyzed the livers for seven rodenticides (brodifacoum, bromadiolone, chlorophacinone, diphacinone, difethialone, pindone, and warfarin). Of the samples, 70% had detectable residues of at least one rodenticide. The prevalence of brodifacoum was approximately 50% and the prevalence of bromadiolone was approximately 52%. Nine of the birds (approximately 6%) were assigned anticoagulant rodenticide poisoning as the “final cause of death.”

Thomas et al (2011) analyzed data (from the previous 10 years, including from Albert et al (2009)) of 270 birds (including 196 Great Horned Owl and Red-tailed Hawks) from Canada using logistic regression to estimate the probability of rodenticide toxicosis at various levels of second generation anticoagulant rodenticides. They found that approximately 65% of the Great Horned Owls and Red-tailed Hawks had residues of at least one second generation anticoagulant rodenticide and that approximately 11% of Great Horned Owls were at risk of dying directly due to the effects of second generation anticoagulant rodenticides.

Lambert el al (2007) collected 58 dead birds (including raptors and water birds) from Loire Atlantique, France, conducted necropsies on them, and had their livers analyzed for five rodenticides, including brodifacoum, bromadiolone, and difenacoum. Bromadiolone residues were found in 26% of the animals and difenacoum residues were found in approximately 14% of the animals. Based on the results of the necropsies, none of the animals appeared to have died directly from anticoagulant rodenticide toxicity.

Summary

The above data indicate that non-target animals from locations outside of California have also been impacted by second generation anticoagulant rodenticides.

Appendix II: Additional Information and Data in California

Additional California data that did not fit easily into DPR's main analysis and/or needed additional explanation are summarized in this section:

Reptiles

Measurable levels of difethialone were found in a gopher snake in the Los Angeles area (Klein Sereiys (2012)). Fisher and Saunders (2012) found that Galapagos tortoises were unlikely to consume brodifacoum. However, Hoare and Hare (2006) found that 2 species of New Zealand geckos would consume bait. Spurr (1993) reported a case where over 100 skinks (*Leiolopisma otagense* and *L. grande*) were found dead after an eradication effort using brodifacoum. Harper et al (2011) found a mortality rate of approximately 5% among Galapagos land iguanas after an eradication program for the black rat (*Rattus rattus*) using brodifacoum on Seymour Norte, Galapagos. Eason and Spurr (1995) concluded that reptiles and amphibians "may be at risk from secondary poisoning" especially if they consumed invertebrates that had fed on brodifacoum. This data indicates that reptiles may also be impacted by anticoagulant rodenticides.

Fetal and neonatal data

The fetus of a bobcat that was hit by a car in the Los Angeles area contained residues of brodifacoum and diphacinone (Klein Sereiys (2012)). Additionally, 1 of 4 fisher kits (that were nursing as their sole source of nutrition) contained trace levels of brodifacoum (Gabriel et al (2012)). The bobcat and kit data suggest that neonatal and lactation transfer are two additional possible routes of exposure for anticoagulant rodenticides that may result in impacts to wildlife.

To date, very few studies have looked at rodenticide residues in fetuses or in newly whelped or hatched animals. In humans, anticoagulants are known to induce two different effects, depending on the time of exposure. Fetal warfarin syndrome is characterized by nasal hypoplasia, causing respiratory difficulty. Fetal wastage results in nervous system, skeletal, and ophthalmological abnormalities causing blindness, low birth weight, and developmental delays (Howald (1997)).

Munday and Thompson (2003) found that two newly whelped puppies that died shortly after birth had brodifacoum residues and showed signs of rodenticide toxicity. The puppies had signs of coagulopathy and were statistically significantly smaller than the unaffected puppies, even though the dam and five unaffected puppies were clinically normal. The authors stated that, "the dam was unaffected, suggesting that fetuses are more susceptible to brodifacoum toxicity than adult animals." If this is the case, then even healthy animals that have residues of anticoagulant rodenticides and are pregnant might lose their offspring due to the effects of the rodenticides.

Naim et al (2011) compared the breeding performance of Barn Owls in Oil Palms that were in an untreated control or had been treated with warfarin, brodifacoum, or a bio-rodenticide (*Sarcocystis singaporensis*, a parasitice protozoon) in three successive seasons. The researchers found no difference in the clutch size based on treatment. However, there was a statistically significant difference in hatching success. Brodifacoum resulted in a hatching success rate of approximately 43%, whereas the control showed a hatching success rate of approximately 84%. Fledging success was also statistically different among the 4 treatments, with the control showing approximately 78% success and those exposed to brodifacoum showed 10% success. In all three seasons, brodifacoum was correlated to the lowest hatching and fledging success (statistically significant from all other treatments at $p<0.05$).

Difethialone in Hawks and a Fox in San Francisco
In San Francisco's Golden Gate Park, 4 hawks and a fox appear to have been affected by "ingesting rats poisoned by difethialone that was used to control rodents in the park." Three of the hawks and the fox are believed to have died as a result of ingestion. The forth hawk was sent to a wildlife rehabilitation center for treatment and was released (Kay (2007a) and Kay (2007b)). The laboratory and necropsy data were not available for analysis.

Summary
These data indicate that reptiles and amphibians, and fetuses and newly born/ hatched animals may also be impacted by anticoagulant rodenticides. The data indicate that rodenticides are able to pass the placental barrier.

Appendix III: Fishers and Badgers in California

DPR recently received data from the analysis of 64 mustelids (fishers and badgers) in California.

Analysis

The data were collected between 2005 and 2011, and came from Gabriel et al (2012a) and Quinn et al (2012). The analysis includes data on 58 fishers and six badgers.

The livers of each animal were analyzed for seven anticoagulant rodenticides. The animals were analyzed for first generation anticoagulant rodenticides - chlorophacinone, coumachlor, diphacinone, and warfarin-- and second generation anticoagulant rodenticides -- brodifacoum, bromadiolone, and difethialone.

Of the 64 non-target animals analyzed, 75.0% had residues of at least one second generation anticoagulant rodenticide. Brodifacoum residues were found in approximately 73% of the animals, bromadiolone residues were found in approximately 30% of the animals, and difethialone residues were found in approximately 2% of the animals. Table 1 summarizes the results.

Table 1. Number (and percent) of the rodenticides among fishers and badgers (n=64) and among positive fishers and badgers (n=50)[1].

Total	Number	Second Generation Anticoagulant Rodenticides			First Generation Anticoagulant Rodenticides		
Samples	64	48 (75.0%)			>8 (>12.5%)		
Positives	50	48 (96.0%)			>8 (>16.0%)		
Total	Number	Brodifacoum	Bromadiolone	Difethialone	Chlorophacinone	Diphacinone	Warfarin
Samples	64	47 (73.4%)	19 (29.7%)	1 (1.6%)	4 (6.3%)	8 (12.5%)	1 (1.6%)
Positives	50	47 (94.0%)	19 (38.0%)	1 (2.0%)	4 (8.0%)	8 (16.0%)	1 (2.0%)

1. Animals may be positive for more than one rodenticide.

Necropsies

Out of the 64 animals analyzed for rodenticides, 58 had necropsies conducted at the California Animal Health and Food Safety Laboratory System (CAHFS) or the Veterinary Medical Teaching Hospital (VMTH), both part of the University of California at Davis located in Davis, California.

A summary of 4 (6.9%) fisher necropsies, where the fishers were most likely killed by anticoagulant rodenticides between 2009 and 2011, were included in the article (Gabriel et al (2012a)). The 4 animals included 2 from the Sierra Nevada population and 2 from the Northern population. Of the 4 animals that most likely died due to anticoagulant rodenticide toxicity, 1 had residues of brodifacoum and chlorophacinone and 3 had residues of bromadiolone and brodifacoum. All 4 had detectable levels of brodifacoum, with the levels ranging from 0.04 to 0.61 ppm.

Location & Land Use
The fishers and badgers came from ten different California counties, including Fresno, Humboldt, Los Angeles, Madera, Mariposa, Monterey, Shasta, Siskiyou, Tehama, and Trinity. The data indicate that fishers and badgers found in rural/agricultural, as well as those found in nature preserves/National Forests, were positive for anticoagulant residues.

Fishers are a candidate for listing under the federal Endangered Species Act in California. They are a medium-sized mammal in the mustelid (weasel) family. They are omnivores, consuming a wide variety of prey (such as rabbits, mice, squirrels, reptiles, amphibians, insects, porcupines, and carrion), as well as fruit, berries, and plants. In California, fishers "are dependent on mid to late-serial stage coniferous and hardwood forests" and often inhabit lands associated with a lack of humans. Gabriel et al (2012) used spacial analysis and found that exposure was widespread and not isolated to areas of known human activity. They came to the conclusion that a "likely source of AR exposure to fishers is… illegal marijuana cultivation." This was supported by spacial analysis, the timing of the mortalities, and raids in areas surrounding the mortalities (Gabriel et al (2012a), Gurrola (2010), and USDA Forest Service (2011)).

The population of the fishers in the Sierra Nevada is estimated to be 150 to 300 individuals. There is no natural movement to or from the Sierra Nevada population to other populations (including the Northern California population), so individuals are gained through birth and lost through death. Forty (40) animals were analyzed from the southern Sierra Nevada population. Of these, 33 (82.5%) of the fishers were exposed to anticoagulant rodenticides, 32 (80.0%) were exposed to brodifacoum, 14 (35%) were exposed to bromadiolone, and 1 was exposed to difethialone. Two (5%) of the fishers died due to second generation anticoagulant rodenticide toxicity.

American badgers are primarily carnivorous, preferring to eat small burrowing mammals such as moles, ground squirrels, rats, mice, and gophers. They live in open areas (i.e., not forests or urban areas), including grasslands, parks, and farms. Data indicate that 4 of the 6 badgers were positive for second generation anticoagulant rodenticides, including 3 (50.0%) which were positive for brodifacoum, 3 (50.0%) which were positive for bromadiolone and 2 (33.3%) which were positive for both brodifacoum and bromadiolone.

Summary
These data further support DPR's assertion that exposure and toxicity to non-target wildlife from second generation anticoagulant rodenticides is a statewide problem, and that the use of second generation rodenticides presents a hazard related to persistent residues in target animals resulting in impacts to non-target wildlife.

Amphibians and reptiles associated with the prairie dog grasslands ecosystem and surrounding areas at the Janos Casas Grandes complex, northwestern Chihuahua, Mexico

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AMPHIBIANS AND REPTILES ASSOCIATED WITH THE PRAIRIE DOG GRASSLANDS ECOSYSTEM AND SURROUNDING AREAS AT THE JANOS CASAS GRANDES COMPLEX, NORTHWESTERN CHIHUAHUA, MEXICO

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RESUMEN

Los perros de las praderas (*Cynomys ludovicianus*) se consideran actualmente una especie clave, ya que forman extensas colonias que se caracterizan por presentar una gran diversidad de vertebrados asociados a ellas. Las colonias más grandes de esta especie en Norteamérica se localizan en la región de Janos, al noroeste de Chihuahua, México. En este estudio presentamos un inventario de las especies de anfibios y reptiles que habitan en los pastizales de esta región así como de los matorrales de mesquite aledaños a las colonias de perros de las praderas. Los métodos de estudio incluyeron la utilización de un sistema de trampas de caída ordenadas en cuadrícula así como el registro de encuentros visuales (VES) mediante caminatas diurnas y nocturnas. Se registraron 9 especies de anfibios y 35 de reptiles, de estas especies, 28 están definitivamente asociadas con las colonias de perros de las praderas, y 18 especies se encontraron exclusivamente en este ambiente. Por otro lado, encontramos que 13 especies habitan exclusivamente en el matorral de mesquite. Las comunidades de anfibios y reptiles en la región de Janos tienen gran importancia para la conservación ya que 16 especies de esta diversidad (1 de anfibio y 15 de reptiles) se consideran en alguna categoría de conservación. La diversidad de la herpetofauna encontrada en los pastizales de Janos es relativamente alta comparada con la de otras colonias de perros de la pradera de Norte América. Con este estudio confirmamos que las colonias de perros de las praderas son un factor importante para el sostenimiento de la diversidad biológica en los pastizales del noroeste de México y Norte América en general, tal como se observó con los mamíferos y las aves del desierto Chihuahuense.

Palabras clave: Anfibios y reptiles, colonias de perros de las praderas, pastizales, diversidad biológica, Chihuahua.

ABSTRACT

Prairie dogs (*Cynomys ludovicianus*) are considered a keystone species that forms extensive colonies in the grasslands of western and central North America. These colonies are characterized by high diversity of associated vertebrates. The largest colonies in North America are located in the Janos region, northwestern Chihuahua, Mexico. In this study we present an inventory of the amphibians and reptiles inhabiting at prairie dog grasslands and surrounding mesquite scrublands in the Janos region. Methods to assess the herpetofauna included the use of a combined system of pitfall traps and visual encounter surveys (VES). We found 9 species of amphibians and 35 of reptiles. Of these species, 28 were closely related to prairie dog colonies, and 18 were exclusively recorded in this habitat.

Additionally, 13 species were restricted to the mesquite scrubland. The Janos amphibian and reptile communities are of conservation concern, because 16 of the included species (1 amphibian and 15 reptiles) are considered at some risk of extinction. The diversity of amphibians and reptiles in the Janos region is clearly high in comparison with other grasslands. Our results strongly support the assumption that prairie dog grasslands are important for maintaining the mammal and avian diversity in the ecosystems of the Chihuahuan desert.

Key words: Amphibians and reptiles, prairie dog colonies, grasslands, biological diversity, Chihuahua.

INTRODUCTION

Grasslands are among the most threatened ecosystems in North America, mainly because of land use changes that have transformed the landscape in a disturbed mosaic of grasslands immersed in a matrix of agricultural and pasture lands (Ceballos *et al*. 2005). The black–tailed prairie dog (*Cynomys ludovicianus*) is a species that once occupied the grasslands of a vast region from southern Canada to northern Mexico. The advance of cattle and agricultural activities have reduced prairie dog distribution to 2 to 5% of their originally range (Miller *et al*. 1994, Marce-Santa, pers. comm.). Prairie dogs play an important role in the structure and function of the grassland ecosystem because of its influence in maintaining regional and local species diversity, to the point that they are considered keystone species in these ecosystems (Lomolino & Smith 2003, Ceballos *et al*. 2005). However, very few large prairie dog colonies persist in North America. The most important remaining colony, covering 250,000 ha, is located in the Janos–Casas Grandes complex (JCGC) at northwestern Chihuahua, Mexico. We evaluated the vertebrate diversity in this grasslands-prairie dog ecosystem, as well as the semi arid mesquite scrublands of the Janos-Casas Grandes region as part of a major project aimed to understand the relationship between the prairie dog ecosystem and related vertebrate diversity (Pacheco *et al*. 2000, Manzano-Fischer *et al*. 1999, Ceballos *et al.* 2005, Manzano-Fisher *et al.* 2006). The Janos-Casas Grandes region belongs to the Chihuahuan biotic province recently identified as a highly endemic area for amphibians and reptiles in northern Mexico (Ochoa-Ochoa & Flores-Villela 2006). The biological information concerning the amphibians and reptiles in northwestern Chihuahua is scarce, previous inventories in the state have mainly focused on the montane forests, desert, and scrubland areas from central and eastern Chihuahua (Tanner 1985, 1987, 1989, Lemos-Espinal, *et al.* 2004, Lemos Espinal & Smith 2007), with little or incidental information on grasslands occupied by prairie dog colonies in the extreme northwestern areas of the state (e. g. Domínguez *et al.* 1974). In contrast, there are some studies on the herpetofauna associated with prairie dog colonies in the US that have well documented the association of mammals and birds -and to a lesser degree the amphibian and reptile communities- to the prairie dog colonies (e.g. Campbell & Clark 1981, Sharp & Uresk 1990, Kretzer & Cully 2001, Lomolino & Smith 2003). The main intent of this paper is to report the results of an inventory of species of amphibians and reptiles associated to the grasslands and scrublands at the Janos region, we also discuss on conservation aspects of the amphibian and reptile species in this region.

Study area. The study area is located in the Janos Municipality in extreme northwestern Chihuahua, Mexico, about 60 km south of the border with the United States of America (30° 55’ 07’’ N; 108° 29’ 59’’W; Fig. 1). The whole area encompasses about 50,000 ha, with elevation ranging from 1,300 to 1,450 m. Climatic conditions can be described as temperate and dry seasonal with rainfalls in summer (three months), a long dry season (eight months), and a growing season of about 200 days (Royo-Márquez & Báez-González 2001). The average annual temperature is 15.7° C with a difference of 14° C between the coldest and hottest months; annual average precipitation is 306.7 mm with a constant low atmospheric

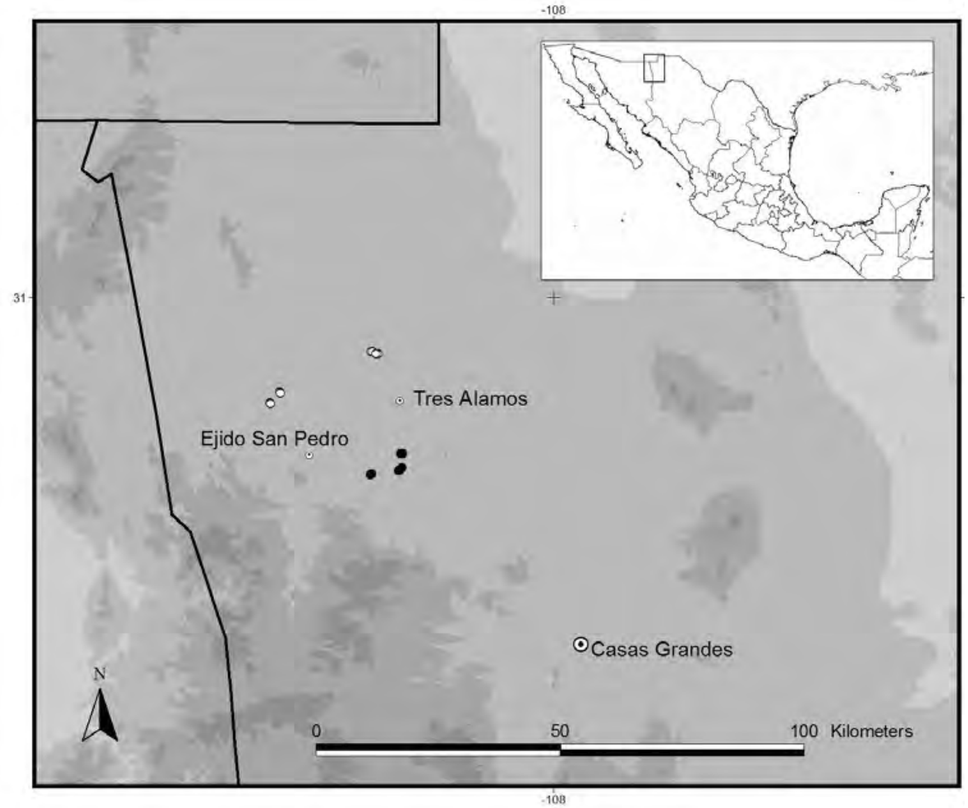

Figure. 1 Location of the Janos-Casas Grandes Complex and the grassland (black circles) and scrubland (open circles) sites sampled in this study.

humidity (Garcia, 1981). The landscape consists of moderate open grasslands and scrublands. The plant composition of the prairie dogs colonies is of abundant grasses (e.g. blue gramma, *Bouteloua gracilis*, and black gramma, *B. eripoda*) with some areas supporting a high concentration of longleaf jointfir (*Ephedra trifurca*), Snakeweed (*Gutierrezia imbricata*), and cholla cactus (*Opuntia imbricata*) (Royo-Márquez & Báez-González 2001). Scrublands are dominated by white thorn acacia (*Acacia constricta*), mesquite (*Prosopis* sp.), and cat-claw (*Mimosa biuncifera*). The riparian communities are composed of large trees such as sycamore (*Platanus wrightii*), Arizona walnut (*Junglans major*), and willows (*Salix* sp.). The area has been inhabited for more than 50 years by a Menonite community; their main activities are agriculture and livestock. In last decade electricity was introduced in these settlements causing an important negative synergistic impact to the natural systems related to the modernization of the traditional agricultural activities (Cartron *et al*. 2005; Ceballos *et al.* 2005).

MATERIAL AND METHODS

The inventory of species of amphibians and reptiles in the Janos region started informally in 1997, when the first records were compiled from transects along the area. The systematic study of the herpetological populations began on 2001 when we conducted six sampling periods including 2002 and 2004. We conducted two sample periods in each of the following years covering wet and dry seasons: 2001 (May, June), 2002 (June, September) and 2004 (April, July). For the regional inventory we studied 8 sites of grassland and 8 sites of scrubland, with additional records observed at the riparian adjacent areas. Two sampling techniques were conducted at each site. First, individual visual encounter surveys (VES) were made with two observers walking north–south direction along 1 km x 10 m diurnal transects (transects reduced to 1 km x 6 m for nocturnal surveys); distance between observers was 50 m. Diurnal surveys were conducted between 0900–1200 hr, and nocturnal surveys between 2000–2300 hr. Transects were run during three day periods, resulting in 72 hours/person/site sampled. Additionally, we established a system of pitfall-trap grids in each of the 16 grassland and mesquite scrubland sites. Each system consisted of 9 pitfall traps arranged in a 3 X 3 trap grid separated by a distance of 30 m to cover a total area of 360 m^2. Each trap consisted of a standard plastic bucket (19 liters/capacity; Heyer *et al*. 1994). The system remained opened for three consecutive days in each sampling season. Each site was checked every morning or twice a day on extremely hot days. In order to avoid animal mortality due to the intense high temperatures, a wood cover was placed over the trap (Corn 1994). Linear transects were always located in areas adjacent to the trap grids. Specimens were captured in the study sites directly by hand, identified, examined, and then released. All individuals observed were marked according to the standard toe clipping system for anurans and lizards, and scale remove for snakes (Heyer *et al.* 1994), however data concerning changes in density population data will be reported in other paper dealing on abundance and interactions with other vertebrates (Davidson *et al.* in prep). Representative voucher specimens of each species were collected, preserved, and deposited in the Herpetological Collection, Museo de Zoología, Facultad de Ciencias, UNAM (MZFC). Almost all the species listed in this study are the result of our field observations. Non-literature records exist for this specific area, the nearest records come from surroundings Janos and are commented in the Discussion. A cumulative species curve was constructed by using records since 1997 to date for inventory purposes only. Nomenclature for the species list follows those of Flores-Villela, (1993), Flores-Villela & Canseco-Márquez (2004), Frost (2007) and Liner (2007).

RESULTS

Species richness and composition. We recorded 44 species of amphibians and reptiles, comprising 9 species of amphibians (20.5%) and 35 of reptiles (79.5%), and representing 5 and 22 genera and 3 and 11 families, respectively (Appendix 1). However, the cumulative species curve suggests that the inventory of herpetofauna remains incomplete (Fig. 2). Non-endemic species for Mexico occurs in this region, however five species and subspecies, such as the Chihuahuan collared lizard (*Crotaphytus collaris*), are endemic to the Chihuahuan desert.

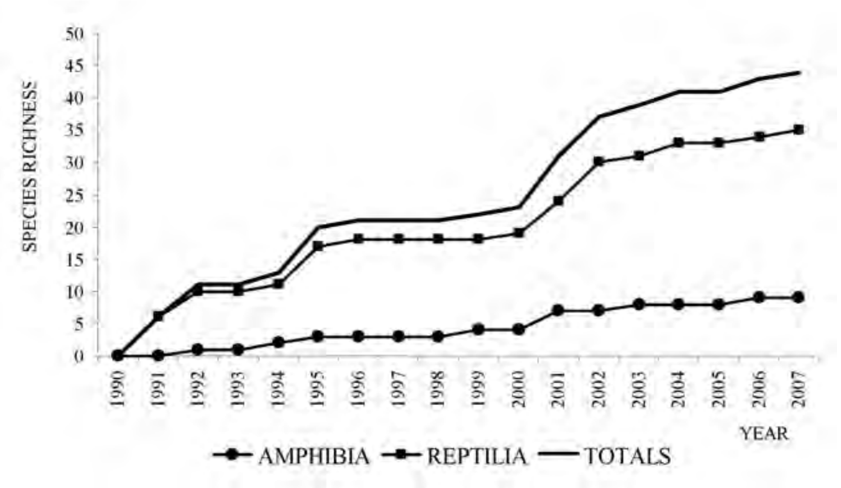

Figure. 2 Cumulative number of species of amphibians (X) , reptiles (open triangles) and the whole herpetofauna (open squares) recorded in last decade at the Janos–Casas Grandes Complex, northwestern Chihuahua, Mexico.

Distribution across habitats and seasonality. The distribution of species across habitats was heterogeneous. Seven species, such as the green toad (*Anaxyrus debilis*), the Western earless lizard (*Holbrookia approximans*), and the Mojave rattlesnake (*Crotalus scutulatus*), were generalists, found in both grassland and scrubland habitats; *C. scutulatus* was found even in the riparian habitat. Grasslands with prairie dogs supported 30 species of amphibians an reptiles (68.2%). Six amphibians and 17 reptiles are exclusive of this ecosystem, like the Colorado River toad (*Ollotis alvaria*), the Horned lizard (*Phrynosoma hernandesi*), and the Ground snake (*Sonora semiannulata*, Appendix 1). In the mesquite scrubland we recorded 19 species (43.2%) including 3 amphibians and 16 reptiles; 12 of those species such as the Spade foot toad (*Spea bombifrons*), the Texas horned lizard (*Phrynosoma cornutum*), and the Long-nosed snake (*Rhinocheilus lecontei*), were recorded exclusively in this last habitat. Two species of reptiles, the Southwestern fence lizard (*Sceloporus cowlesi*), and the Yellow mud turtle (*Kinosternon flavescens*) were recorded exclusively at the riparian habitat (Appendix 1).

The activity of amphibians was recorded during two complete seasons being higher at the rainy season, when most of the species were breeding in the temporal pools formed after heavy rainfalls (July–September; Santos & Pacheco, 2004). Reptiles showed a higher activity in this season too, probably because of the abundance of insects and other small vertebrates such as mice and small lizards that represent the main part of the diet of snakes. Through the dry season (December–March), the activity of amphibians and reptiles decreased considerably in both grasslands and scrublands, and only 5 species of reptiles were observed in low abundances (Fig. 3).

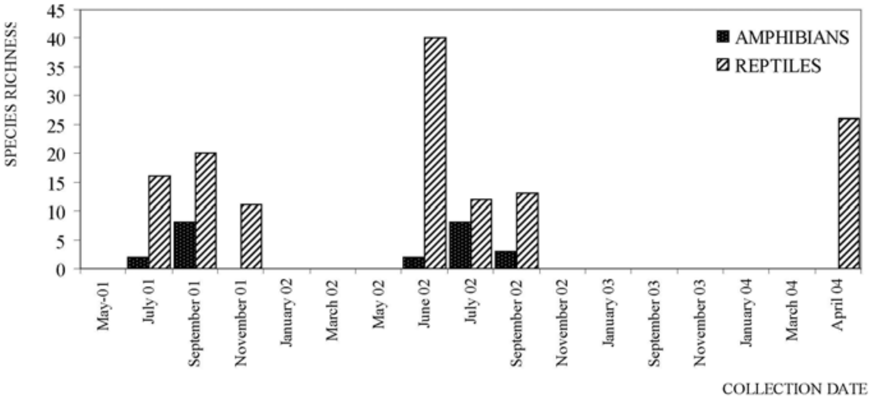

Figure 3. Seasonal activity of amphibians and reptiles during two and a half years of observations at the grasslands and scrublands of the Janos-Casas Grandes Complex.

DISCUSSION

Diversity and conservation status of the herpetofauna. According to the cumulative species curve the diversity of the herpetofauna in the area is probably higher than indicated by our inventories. We think that the only under-represented group in this study are the snakes, which because of their habits are difficult to observe. Some species like the Southwestern black-headed snake (*Tantilla hobartsmithi*) were recorded only with the pitfall traps and some snake species were recorded just once. The regional diversity can increase because there are other species recorded at some surrounding Janos localities (i.e. Domínguez *et al.* 1974, Lemos-Espinal *et al.* 2004, Lemos Espinal & Smith 2007). Two species of amphibians of probable occurrence, but never seen in this study, are the Tiger salamander (*Ambystoma velasci, formerly A. tigrinum*), a species commonly found in the grasslands in west central and southwestern US, and the Lowland leopard frog (*Lithobates yavapaiensis*), this last species possibly occurring in the mountain streams at northern Sierra de San Luis. Regarding reptiles there are other species of probable occurrence in the region as the Gila monster (*Heloderma suspectum*), rarely present in grasslands and woodlands but common in scrublands, and the Madrean alligator lizard (*Elgaria kingii*), a common inhabitant of the foothills in the forests of southwestern New Mexico (Degenhardt *et al.* 1996). We attribute the lack of records of these species in the grasslands to their habits; both are usually more common in foothill and rocky habitats than in lower plains. It is important to note that only grassland and scrubland species were reported in this study, however the regional diversity increases when expanded to include more montane habitats. Here, species such as the Rock rattlesnake (*Crotalus lepidus*), the Ridgenose rattlesnake (*C. willardi*), and the Tree lizard (*Urosaurus ornatus*) can be found in the margins between grasslands and foothills.

The Colorado River toad (*Ollotis alvaria)* is a new record for the State of Chihuahua, having previously considered to be confined to the Sonoran desert region (Santos-Barrera *et al.* 2006); this species was not included in the last published compilation of records of amphibians and reptiles of Chihuahua (Lemos-Espinal & Smith 2007). Concerning the red spotted toad (*Anaxyrus punctatus)*, the nearest known records in Chihuahua are located southward, near the city of Casas Grandes, and to the North in extreme southwestern New Mexico (Dehgenhart *et al*. 1996).

Fifteen species occurring at the Janos region are listed in the Red Data Book of México, (NOM-059, SEMARNAT 2003) and should be considered for conservation priority. The Janos region is a critical habitat for some species, like the green toad (*Anaxyrus debilis*) because there exist healthy and stable populations (Santos-Barrera & Pacheco 2004). Other species require population assessments in order to define their present conservation status, including the Ornate box turtle (*Terrapene ornata*), and the Massasuga (*Sistrurus catenatus*); both are common inhabitants of the grasslands and considered under the Special Protection Category (SEMARNAT, 2003).

Our results show similar trends in relation to other studies assessing the vertebrate fauna associated with prairie dog colonies in North America. Most studies have found a higher diversity in areas with prairie dog grasslands in comparison with grasslands and scrublands without prairie dogs (e.g. Campbell & Clark 1981, Sharps & Uresk 1990, Miller *et al.* 1994, Manzano-Fisher *et al.* 1999, Kretzer & Cully 2001, Lomolino & Smith, 2003, Shipley & Reading 2006). Aside from having a high diversity of reptiles and amphibians, the prairie dog grasslands and adjacent habitat types in Janos also support a high diversity of other vertebrates, especially birds and large carnivores (Manzano-Fischer *et al.* 1999; 2007, Pacheco *et al.* 2000). Further research at prairie dogs colonies and surroundings in northern Chihuahua is still necessary to confirm the presence of other species to evaluate the present conservation status of the amphibians and reptiles in the area. Our results indicate that the prairie dog grasslands of the Janos-Casas Grandes complex support the highest diversity of amphibians and reptiles in all North American prairie dog colonies yet studied. Any efforts to protect this area would help to preserve an important ecosystem and a significant part of the native flora and fauna in northern Mexico.

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LITERATURE CITED

Campbell, T. M. & T. W. Clark. 1981. Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. *American Midland Naturalist*, 105: 269-276.

Cartron, E. J., R. E. Harness, R. C. Rogers & P. Manzano-Fisher. 2005. Impact of concrete power poles on raptors and ravens in northwestern Chihuahua, Mexico. Pp. 357-369. 438 *In*: Cartron, J.E., G. Ceballos and R. S. Felger (Eds). *Biodiversity, ecosystems and conservation in Northern Mexico*. Oxford University Press, New York.

Ceballos, G., R. List, J. Pacheco, P. Manzano-Fischer, G. Santos & M. Royo. 2005. Prairie dogs, cattle, and crops: diversity and conservation of the grassland-shrubland habitat mosaic in northwestern Chihuahua. Pp. 425-438 *In*: Cartron, J.E., G. Ceballos and R. S. Felger (Eds). *Biodiversity, ecosystems and conservation in Northern Mexico*. Oxford University Press, New York.

Corn, S. P. 1994. Straight-line drift fences and pitfall traps. Pp. 109-117 *In*: Heyer, W. R., M. A. Donelly, R. W. McDiarmid, L.C. Hayek & M. S. Foster (Eds). *Measuring and monitoring biological diversity. Standard methods for amphibians*, Smithsonian Institution Press, Washington, D. C.

Degenhardt, W. E., C. W. Painter & A. H. Price. 1996. *Amphibians and reptiles of New Mexico*. University of New Mexico Press. Albuquerque. 431 pp.

Domínguez, P., T. Alvarez & P. Huerta. 1974. Colección de anfibios y reptiles del noroeste de Chihuahua, México. *Revista de la Sociedad Mexicana de Historia Natural*, 35: 117-142.

Flores-Villela, O. A. 1993. Herpetofauna Mexicana. *Special Publications of the Carnegie Museum of Natural History*. No. 17. 1-73.

Flores-Villela, O. A. & L. Canseco Márquez. 2004. Nuevas especies y cambios taxonómicos para la herpetofauna de México. *Acta Zoológica Mexicana (n.s.)* 20: 115-144.

Frost, D. R. 2007. Amphibian Species of the World: an Online Reference. Version 5.1 Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.php. American Museum of Natural History New York, USA.

Garcia, E. 1981. *Modificaciones al Sistema de Clasificación Climática de Köppen*. Instituto de Geografía. UNAM. 252 pp.

Heyer, W. R., M. A. Donelly, R. W. McDiarmid, L.C. Hayek & M. S. Foster (Eds). 1994. *Measuring and monitoring biological diversity. Standard methods for amphibians*, Smithsonian Institution Press, Washington, D. C.

Kretzer, J. E. & J. F. Cully. 2001. Effects of black-tailed prairie dogs on reptiles and amphibians in Kansas short grass prairie. *Southwestern Naturalist*, 46: 171-177.

Lemos-Espinal, J. A., H. M. Smith & D. Chiszar. 2004. *Introducción a los anfibios y reptiles del Estado de Chihuahua*. UNAM-CONABIO, México, D. F. 128 pp.

Lemos-Espinal J. A., & H. M. Smith. 2007. *Anfibios y reptiles de Chihuahua*. UNAM-CONABIO, México D. F., 613 pp.

Liner, E. 2007. A checklist of the amphibians and reptiles of Mexico. *Occ. Paps. Museum National Science of Lousiana State University* No. 80: 1-60.

Lomolino, M. V. & G. A. Smith, 2003. Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. *Biological Conservation*, 115:89-100.

Manzano-Fischer, P. R. List & G. Ceballos. 1999. Grassland birds in prairie-dog towns in Northwestern Chihuahua, Mexico. *Studies on Avian Biology*, 19: 263-271.

Manzano Fischer, P. R. List, G. Ceballos, & J. L. Cartron. 2006. Avian diversity in a priority area for conservation: the Janos - Casas Grandes Prairie Dog Complex and adjacent habitats of Northwestern Mexico. *Biodiversity Conservation* 15:3801-3825.

Miller, B, G. Ceballos & R. Reading. 1994. The prairie dog and biotic diversity. *Conservation Biology*, 8: 677-681.

Ochoa-Ochoa, L. M. & O. Flores-Villela. 2006. *Áreas de diversidad y endemismo de la herpetofauna mexicana*. UNAM-CONABIO, México, D. F. 211 pp.

Pacheco, R. J., G. Ceballos & R. List. 2000. Los mamíferos de la región de Janos-Casas Grandes, Chihuahua, México. *Revista Mexicana de Mastozoología*, 4: 71-85.

Royo-Márquez, M. & A. D. Báez-González. 2001. Descripción del hábitat de áreas colonizadas y sin colonizar por perrito llanero (*Cynomys ludovicianus*) en el noroeste de Chihuahua. *Técnicas Pecuarias de México,* 39 (2): 89-104.

Santos-Barrera, G. & J. Pacheco. 2004. Status of three species of toads in northwestern Mexico. *Froglog*, 63: 1-2.

Santos-Barrera, G., J. Cruzado, E. Ponce Guevara, R. Sierra & J. Pacheco. 2006. *Bufo alvarius* (Sonoran desert toad) Geographic Distribution. *Herpetological Review*, 37: 98.

SEMARNAT, 2003. *Norma Oficial Mexicana NOM-059-ECOL-2001*, Protección ambiental- Especies nativas de México de flora y fauna silvestres- Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. Diario Oficial de la Federación 582: 1-80.

Sharp, C. C. & D. W. Uresk. 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. *Great Basin Naturalist*, 50: 339-345.

Shipley, B. K. y R. P. Reading. 2008. A comparison of herpetofauna and small mammal diversity of black-tailed prairie dogs (*Cynomys ludovicianus*) colonies and non-colonized grasslands in Colorado. *Journal of Arid Environments*, 66: 27-41.

Tanner, W. W. 1985. Snakes of western Chihuahua. *Great Basin Naturalist*, 45: 615-676.

_______. 1987. Lizards and turtles of western Chihuahua. *Great Basin Naturalist*, 47: 383-421.

_______. 1989. Amphibians of western Chihuahua. *Great Basin Naturalist*, 49: 38-70.

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Appendix 1

Species of reptiles and amphibians recorded in the Janos-Casas Grandes region, Chihuahua, Mexico. HABITAT: G, grassland; S, scrubland; R, riparian. ABUNDANCE: R: rare; C: common; A, abundant. CONSERVATION (NOM 059, SEMARNAT, 2003): T =threatened; Pr = Under special protection. Taxonomy follows those of Flores Villela (1993); Flores Villela y Canseco Márquez, (2004), Frost (2007), and Liner (2007).

	HABITAT	ABUNDANCE	CONSERVATION
Amphibia			
Anura			
Bufonidae			
Ollotis alvaria	G	R	
Anaxyrus cognatus	G	A	
Anaxyrus debilis	G/S	A	Pr
Anaxyrus punctatus		R	
Anaxyrus woodhousei	G	A	
Pelobatidae			
Scaphiopus couchi	G	C	
Spea bombifrons	S	C	
Spea hammondi	G	C	
Ranidae			
Litobathes catesbeiana	G	R	
Reptilia			
Squamata			
Crotaphytidae			
Crotaphytus collaris	G	R	T
Phrynosomatidae			
Holbrookia approximans	G/S		A
Phrynosoma cornutum	S	C	T
Phrynosoma hernandesi	G	R	
Phrynosoma modestum	S	R	
Sceloporus magister	S	R	
Sceloporus poinsetti	G	R	
Sceloporus scalaris	S		A
Sceloporus cowlesi		R	C
Uta stansburiana	S	A	T
Scincidae			
Plestiodon obsoletus	S	R	
Teiidae			
Aspidoscelis exsanguis	G/S	A	
Aspidoscelis tigris	S		C
Aspidosceliss uniparens	G/S	A	

	HABITAT	ABUNDANCE	CONSERVATION
Colubridae			
Arizona elegans	S	R	
Coluber flagellum	G	R	T
Diadophis punctatus	G	R	
Heterodon kennerly	G	R	Pr
Lampropeltis getula	G/S	R	T
Pituophis catenifer	G/S	A	
Rhinocheilus lecontei	S	R	
Salvadora deserticola	S	R	
Sonora semiannulata	G	R	
Tantilla hobartsmithi	G	C	
Tantilla nigriceps	G	C	
Thamnophis cyrtopsis	G	R	T
Thamnophis eques	G	R	T
Thamnophis marcianus	G	R	T
Crotalidae			
Crotalus atrox	G	C	Pr
Crotalus molossus	G	R	Pr
Crotalus scutulatus	G/S	C	Pr
Crotalus viridis	G	A	Pr
Sistrurus catenatus	G	R	Pr
Testudines			
Emydidae			
Terrapene ornata	G	C	Pr
Kinosternidae			
Kinosternon flavescens	R	R	

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Invited Paper

Wildlife Conservation Planning Under the United States Forest Service's 2012 Planning Rule

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ABSTRACT In 2012, the United States Forest Service (USFS) promulgated new planning regulations in accordance with the National Forest Management Act (NFMA). These regulations represent the most significant change in federal forest policy in decades and have sweeping implications for wildlife populations. We provide a brief overview of the history of the NFMA planning regulations and their wildlife provisions and review the current science on planning for effective wildlife conservation at the landscape scale. We then discuss the approach to wildlife conservation planning in the 2012 rule and compare it to alternatives that were not selected and previous iterations of the planning rule. The new planning rule is of concern because of its highly discretionary nature and the inconsistency between its intent on the one hand and operational requirements on the other. Therefore, we recommend that the USFS include in the Directives for implementing the rule commitments to directly monitor populations of selected species of conservation concern and focal species and to maintain the viability of both categories of species. Additional guidance must be included to ensure the effective selection of species of conservation concern and focal species, and these categories should overlap when possible. If the USFS determines that the planning unit is not inherently capable of maintaining viable populations of a species, this finding should be made available for scientific review and public comment, and in such cases the USFS should commit to doing nothing that would further impair the viability of such species. In cases where extrinsic factors decrease the viability of species, the USFS has an increased, not lessened, responsibility to protect those species. Monitoring plans must include trigger points that will initiate a review of management actions, and plans must include provisions to ensure monitoring takes place as planned. If wildlife provisions in forest plans are implemented so that they are enforceable and ensure consistency between intent and operational requirements, this will help to prevent the need for additional listings under the Endangered Species Act and facilitate delisting. Although the discretionary nature of the wildlife provisions in the planning rule gives cause for concern, forward-thinking USFS officials have the opportunity under the 2012 rule to create a robust and effective framework for wildlife conservation planning. © 2013 The Wildlife Society.

KEY WORDS at-risk species, coarse-filter, fine-filter, focal species, forest planning, monitoring, viability.

In April 2012, the United States Forest Service (USFS) issued its final planning rule in accordance with requirements of the National Forest Management Act of 1976 (NFMA; 77 FR 21162). The 2012 rule took over 2 years to complete and included extensive public involvement, consultation through forums with scientists and policy experts, and environmental analysis conducted in accordance with the National Environmental Policy Act of 1969 (NEPA; USFS 2012). The new rule represents the most substantive change in federal forest policy in 30 years, with sweeping implications for wildlife. We review the administrative history of the planning rule, explore the provisions that affect the conservation of wildlife and biodiversity, and discuss how careful implementation could lead to more efficient and effective wildlife management. To provide a context for interpreting the changes that will come with implementation of the new rule, we begin with a short administrative history, and then provide a conceptual framework for interpreting the management implications of the rule. We also consider the intersection of the NFMA and the Endangered Species Act (ESA) and look at the implications of this rule change for ESA decision making. We conclude with a series of observations and recommendations for how the wildlife profession might help ensure that sound science and practical policy are effectively wed as the planning rule is implemented across the nation's public forest lands over the years to come.

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A BRIEF HISTORY OF THE 2012 PLANNING RULE

The NFMA created a 3-tiered, regulatory approach to planning. At the highest tier, national-level regulations govern the development and revision of second-tier forest plans. Site-specific plans for projects and other activities make up the third tier, and they must be consistent with both sets of higher-level regulations. Forest plans typically make zoning and suitability decisions and regulate various activities within a forest area, therefore acting as a gateway through which subsequent project-level proposals must pass. They do not, however, authorize or mandate site-specific projects. Instead, plans address issues such as the prioritization of various multiple-use goals, requirements for managing resources such as wildlife, watersheds, or soils, and the determination of which land is suitable for timber cutting, along with allowable volume and the choice of harvesting and regeneration methods.

Efforts to revise the rules governing Forest Service planning have been many, and debate has been intense, resulting in considerable confusion regarding the requirements, process, and legal provisions underlying recent forest planning and management. During development of the 2012 rule, the USFS operated under the 1982 planning rule (47 FR 43026), despite the issuance of more recent rules in 2000 (65 FR 67514), 2005 (70 FR 1023), and 2008 (73 FR 21468). The 2000 rule, developed by the Clinton administration with guidance from a Committee of Scientists (Committee of Scientists 1999), was deemed by the subsequent administration too "costly, complex, and procedurally burdensome" (77 FR 21162: 21164) to implement, and the USFS reverted to planning under the terms of the 1982 rule. Both the 2005 and the 2008 rules were enjoined by the courts because of a failure to meet legal requirements. The agency had argued that planning regulations did not have environmental impacts and thus did not require analysis under the NEPA and the ESA, but this argument failed to survive judicial review (*Citizens for Better Forestry v. USDA* 2007, 2009). A desire to address these persistent weaknesses and to avoid a similar judicial outcome is evident in the language of and justification for the 2012 rule.

One of the most controversial and highly litigated aspects of previous USFS planning rules has been the regulations written in accordance with the NFMA's requirement to "provide for a diversity of plant and animal communities based on the suitability and capability of the specific land area in order to meet overall multiple-use objectives" (16 USC 1604[g][3][B]). To interpret the diversity provision and other requirements of the NFMA, a Committee of Scientists was convened in 1977, in accordance with requirements of the NFMA, to assist with the development of the first planning rule (issued in 1979 and revised in 1982). The diversity regulations in the 1982 rule required that "fish and wildlife habitat shall be managed to maintain viable populations of existing native and desired non-native vertebrate species in the planning area" (36 CFR 219.19). The reference to "viable populations," drawn directly from fundamental principles of population biology, embedded specific, scientific intent into the Forest Service's planning and management responsibilities.

Subsequently, this provision caused significant controversy and drove change in forest management (Corbin 1999, Duncan and Thompson 2006). For example, compliance with the viability provision initiated litigation over the northern spotted owl (*Strix occidentalis caurina*), and led the courts to reject forest plans in the Pacific Northwest for failure to protect the viability, not only of the owl, but also of other species associated with late-successional forests (Duncan and Thompson 2006). Implementation of the 1982 rule relied primarily on the selection of management indicator species, like the northern spotted owl, meant to serve as surrogates to indicate management impacts on a broader suite of unmeasured species. Most forests indirectly assessed the status and trends of management indicator species by measuring habitat amount, a controversial practice that has been the subject of numerous court cases (Corbin 1999). Nonetheless, the use of habitat as a proxy for population status was established in court as not necessarily prohibited by the 1982 regulations (*Inland Empire Public Lands Council v. USFS* 1996).

In the 1990s, the USFS made several attempts to revise the planning rule, and in 1997 a second Committee of Scientists was convened. Its recommendations served as the basis for the 2000 rule, which maintained the viability requirement and extended it to all plant and animal species. The Committee of Scientists suggested a combination of coarse-filter approaches, which focus on the maintenance of ecosystems defined in terms of dominant vegetation types and their successional stages (see Hunter 1990), and fine-filter approaches, which involve direct species-specific measurements of population status and trends (Haufler et al. 1996, Committee of Scientists 1999). Specifically, the 2000 rule required that focal (see below) and at-risk species be monitored using fine-filter approaches. Diversity provisions of the 2000 rule were never implemented, because in 2001 the USFS reverted to the 1982 rule, using a transitional provision in the 2000 rule, while the Bush administration initiated revisions to the planning rule. Both the 2005 and 2008 rules relied entirely upon a coarse-filter approach to wildlife conservation. Contrary to assertions from the scientific community (Noon et al. 2003, 2005), the USFS argued that maintenance of broad ecosystem diversity (as represented by coarse-filter approaches) would adequately protect species and address their diversity obligations under the NFMA. These rules did not require any fine-filter, species-specific planning or monitoring. When the 2005 and 2008 rules were enjoined, the court gave the USFS the option of using the 2000 or the 1982 rule. The USFS chose to use the provisions of the 1982 rule, including the viability provision, through the transitional language in the 2000 rule. In its justification of the most recent planning effort, the USFS claims that the 1982 rule is out-of-date in its scientific foundations, planning procedures, and social values, and is too complex, expensive, and procedurally burdensome to implement (77 FR 21162).

CONCEPTUAL BASIS FOR WILDLIFE CONSERVATION PLANNING

In addressing asserted shortcomings of the 1982 rule, the Forest Service adopts an approach to wildlife conservation that hinges primarily on the assessment, analysis, management, and monitoring of habitat. The 2012 Programmatic Environmental Impact Statement for the planning rule states, "The best opportunity for maintaining species and ecological integrity is to maintain or restore the composition, structure, ecological functions, and habitat connectivity characteristics of the ecosystem. These ecosystem components, in essence, define the coarse-filter approach to conserving biological diversity" (USFS 2012:126). This contrasts with the 1982 and 2000 rules that emphasized population viability.

A Combined Coarse-Filter/Fine-Filter Approach

Most wildlife ecologists believe that effective biodiversity conservation planning requires an appropriate balance between habitat-based, coarse-filter approaches and insights from fine-filter, species-level assessment and monitoring (Noon et al. 2009). The 2012 Programmatic Environmental Impact Statement for the planning rule recognizes the limits of the coarse-filter approach stating, "initially at least, some amount of direct species measurement may be needed to assess the effectiveness of the ecological conditions provided under the coarse-filter approach in achieving the goal of conserving the biological diversity of the area" (USFS 2012:124). The impact statement goes on to propose that fine-filter strategies "can be focused on the few species of special concern whose habitat requirements are not fully captured by coarse-filter attributes." However, this language understates the importance of a complementary fine-filter approach. Research indicates that the coarse-filter approach is unlikely to provide a reliable basis for multi-species conservation planning (Cushman et al. 2008), only limited testing of the approach's validity has occurred (Noon et al. 2009), and the monitoring of a select group of species using a fine-filter approach is necessary to determine the efficacy of coarse-filter approaches (Committee of Scientists 1999, Flather et al. 2009). A recent review of the degree to which coarse-filter models can be used to infer animal occurrence concluded that ". . . the observed error rates were high enough to call into question any management decisions based on these models" (Schlossberg and King 2009:609). These authors went on to state, ". . . [coarse-filter] models oversimplify how animals use habitats, and the dynamic nature of animal populations" (Schlossberg and King 2009:609).

Defaulting to vegetation type as a descriptor of a species' habitat has a long history in ecology. It has been driven largely by pragmatism—vegetation is much easier to measure and characterize than prey resources or nest sites, for example. The practice continues because detailed vegetation maps exist for most of the United States based on either extensive ground-surveys or remotely sensed imagery (e.g., USFS LandFire Program). However, vegetation is often a poor proxy for more influential, but difficult to measure resources, and the frequent failure of vegetation-based habitat models to predict a species' distribution and abundance may be because of limitations of this assumed relationship (Van Horne 2002, Cushman et al. 2008). Even with more detailed data on habitat characteristics, unmeasured and unknown factors will still affect populations. For these reasons, population status of focal and at-risk species must be directly assessed. Therefore, a coarse-filter approach based primarily on dominant vegetation communities will have limited ability to predict the distribution and abundance of many wildlife species and effectively address the diversity provisions of the NFMA; this requires both coarse- and fine-filter approaches.

Selecting Species for Fine-Filter Assessment

Striking a balance between coarse-and fine-filter assessments of biological diversity has challenged forest managers for decades. Even if the fine-filter approach was restricted to vertebrates, monitoring the status of all species is not feasible, thus previous planning rules have restricted USFS requirements to an assessment of a small subset of species occurring across the planning area. This pragmatic constraint was recognized in the 1982 planning rule with the designation of management indicator species, species assumed to reflect the effects of management on their populations as well as the populations of many unmeasured species. However, the notion that a single species can serve as an indicator for a suite of species is an untested premise and generally not supported by research studies or ecological theory (Noon et al. 2009, Cushman et al. 2010). The concept that some species act as direct surrogates of others is untenable unless those species share similar population drivers (Cushman et al. 2010).

Instead of management indicator species, the second Committee of Scientists recommended the use of "focal species" (Committee of Scientists 1999) to evaluate status and trends of plant and animal diversity, generally. The Committee of Scientists proposed that focal species would commonly be selected on the basis of their functional role in ecosystems (e.g., they serve keystone functions [Mills et al. 1993], they are indicators of exposure to key stressors [Caro and O'Doherty 1999], they have a role as engineers of ecological processes [Jones et al. 1994], or play an important role in food web dynamics [Soule et al. 2005]). For federal public lands, Noon et al. (2009) suggest a combined coarse-filter and fine-filter approach, with the latter focusing on monitoring threatened, at-risk, and rare species, along with a modest number of focal species selected with complementary and comprehensive functional roles as described above. Systematic approaches exist for identifying and prioritizing an informative subset of species for fine-filter assessment and monitoring. For example, Regan et al. (2008) suggest selecting species based on existing schemes, such as The World Conservation Union (IUCN) Red List, Nature Serve, Partners in Flight databases, and federal or state listings, combined with an assessment of the degree and spatial and temporal characteristics of known threats. Nevertheless, uncertainties regarding the ability to generalize inferences drawn from any subset of species make the selection process of fundamental importance to the successful implementation of the fine-filter approach.

Improved Techniques for Fine-Filter Monitoring

One argument against direct assessment of wildlife populations is that it is not financially feasible. Traditional monitoring programs and viability analyses have been based on estimates of demographic parameters such as abundance, density, survival, and reproductive rates (Beissinger and McCullough 2002). Estimates of these parameters are expensive, require extensive field surveys, often involve capture and marking of individual animals, and are available for only a small number of species. However, indirect estimates of a species' status and trend based on their spatial distribution can provide defensible surrogate measures (MacKenzie and Nichols 2004, Manley et al. 2004). Focusing on distribution, rather than traditional measures of population size and growth rate, greatly increases the efficiency of broad-scale monitoring programs (Noon et al. 2012). Advancements in wildlife monitoring, based on detection/non-detection data, including the use of sign surveys, genetic evaluation, and historical presence–absence survey data decrease the cost of monitoring changes in distribution, which can be inferred from the proportion of sample units at which the species is detected (MacKenzie et al. 2006). One of the most significant advances in detection/non-detection monitoring is the ability to confirm the presence of a species at a survey site based on its genetic signature (e.g., in hair or scat; Waits 2004, Schwartz et al. 2006). The July 2005 issue of the *Journal of Wildlife Management* devoted a special section to the application of presence–absence sampling in wildlife monitoring (Vojta 2005), including an application to National Forest System lands (Manley et al. 2005). One variable estimated by these models is the area occupied by a species, a measure of a species' spatial distribution. Temporal and spatial patterns in detection/non-detection monitoring data allow inference to changes in animal abundance (MacKenzie and Nichols 2004), the single most influential parameter that provides insights into likelihood of species persistence (Lande 1993). Thus, previous arguments citing the practical limitations of the fine-filter approach are blunted by recent technical and statistical research, much of it inspired by the difficulty and expense of implementing earlier approaches to fine-filter assessments under the 1982 planning rule.

Political and Administrative Barriers to Effective Biodiversity Conservation Planning

In the past, very few if any management indicator species have been monitored in a manner that would allow a reliable assessment of their response to management (Noon et al. 2009). Managers cite the lack of monitoring data as a critical limitation in understanding cumulative impacts to species (Schultz 2012). Aside from cost and the technical challenges discussed above, funding and implementation of reliable, species-specific monitoring has been a significant challenge on National Forest System lands because of political reasons. Maintaining the political and fiscal will to support long-term monitoring programs is difficult (Doremus 2008, Biber 2011). In addition to the challenges of chronic under-funding, management agencies face disincentives to implementing robust species-level monitoring plans because monitoring data may reveal the negative impacts of management. For example, documenting the impacts of timber harvest or fuels reduction activities on sensitive wildlife species often highlights conflicts between different agency mandates, each of which enjoys strong political and social support. In addition, funds allocated to monitoring may draw funds away from projects that result in immediate job creation, the provision of marketable goods such as timber, the attainment of fuels reduction and restoration goals, or other accomplishments that can be reported to Congress in a timely manner. Furthermore, an agency could face legal challenges if it makes enforceable monitoring commitments that it does not have the funding to implement. However, at least as they are typically drafted, monitoring plans are difficult to enforce in court, obviating the need to fully implement intended programs. The judiciary usually finds commitments to monitor land-use plans not subject to review under the parameters of administrative law, and even when reviewed in court, determinations regarding the adequacy of monitoring data are traditionally left to the expertise of administrative agencies (Biber 2011).

Several other issues make understanding management effects on wildlife populations problematic. For example, the USFS has often monitored impacts to species at the project level (Schultz 2010), a spatial scale with generally small population-level effects. Small effect sizes require high statistical power for their detection. The disparity between the scale at which population responses can be detected and the scale of individual management actions leads to persistent problems in assessing impacts to species viability (Ruggiero et al. 1994). Monitoring impacts to habitat must be done cumulatively and at multiple spatial scales to assess whether small-scale habitat changes affect individual organisms, interrupt landscape connectivity affecting multiple populations, or synergistically interact with other small-scale disturbances, resulting in broad-scale effects.

Finally, the integrity of any monitoring plan, coarse- or fine-filter, depends on the articulation of clearly stated objectives and triggers to management actions. A trigger point is a threshold value for a monitoring state variable (e.g., percent area occupied by a given focal species within a national forest planning area) that, when exceeded, triggers a particular management response. A monitoring program without triggers selected a priori to call attention to trends provides little more than a retrospective time series of data with no feedback—and therefore little value—to the management decision-making process (Noon 2003). Furthermore, the efficacy of a monitoring program cannot be assessed at adoption without pre-defined trigger points. Trigger points can be most objectively set up-front, before the difficult management changes that might result from crossing such points are proximate. This is especially true if effects are analyzed exclusively at project scales, masking broader trends. In such cases, declines in population size or habitat quality, for example, may occur incrementally with no recognition of impact until a decline in species status is clearly established via listing under the ESA (Schultz 2010). To provide value to the forest planning process, a monitoring program must establish, a priori, the magnitude of change in the monitoring state variable that would trigger a review of management practices.

In summary, a comprehensive wildlife assessment framework would include a combination of both coarse- and fine-filter approaches. It would commit to monitoring at-risk and focal species using recent advances in monitoring approaches that make species-specific monitoring more financially feasible and efficient than it has been in the past (Noon et al. 2012). As required for effective and meaningful adaptive management, monitoring would occur at multiple spatial scales and use pre-defined triggers to meaningfully evaluate the consequences of management actions and to inform future management decisions.

AN OVERVIEW OF THE 2012 PLANNING RULE'S DIVERSITY PROVISIONS

The planning framework for the 2012 final rule involves a 3-step process: assessment; plan development, amendment, and revision; and monitoring (36 CFR §219.5 [2012]). It requires the use of the "best available scientific information to inform the planning process" (36 CFR §219.3 [2012]) and identifies restoration and watershed protection as agency priorities, while emphasizing the contributions of sound forest management to ecological, social, and economic sustainability (36 CFR §219.8 [2012]). Because restoration requires: 1) an assessment of the current system state relative to desired future conditions; 2) measurement of the system state subsequent to management activities; and 3) a comparison of the observed to desired state, restoration is critically dependent on monitoring. In this section, we discuss the approach in the 2012 rule and the alternatives that were considered but not selected in the agency's decision process.

Assessment and Planning

Section 219.9 outlines the approach for providing for diversity of plant and animal communities. It explains that the USFS is adopting "a complimentary ecosystem and species-specific approach," or a combined coarse- and fine-filter approach. Paragraph (a) outlines the coarse-filter requirements to maintain ecosystem integrity and diversity: plans "must include plan components . . . to maintain or restore the ecological integrity of terrestrial and aquatic ecosystems and watersheds in the plan area" and "maintain or restore the diversity of ecosystems or habitat types throughout the plan area" (ecological integrity and diversity are defined in §219.19 of the 2012 rule). Plan components must function to maintain or restore ecosystem structure, function, composition, connectivity, key ecosystem characteristics, rare species communities, and native tree diversity. A commitment to restore or maintain landscape connectivity to facilitate movement, migration, and dispersal is a significant addition to the planning rule. Paragraph (b) outlines the fine-filter approach. It begins by explaining that the responsible official must determine whether the plan components under part (a), the coarse-filter requirements, will provide the necessary conditions to contribute to the recovery of species listed as threatened or endangered under the ESA, or species that are proposed or candidate species for listing. Additionally, the responsible official must determine whether the coarse-filter approach is sufficient for maintaining viable populations of "species of conservation concern." These are species known to occur in the plan area, other than those listed, proposed, or identified as candidate species under the ESA, that are selected by the Regional Forester based on "substantial concern about the species' capability to persist over the long-term in the plan area" (36 CFR §219.9[c] [2012]). If the coarse-filter is deemed to be insufficient, the responsible official must include species-specific plan components (e.g., buffer areas around nest sites), that will contribute to the recovery of populations of species of conservation concern, as well as federally listed, proposed, and candidate species. If the coarse-filter is assumed adequate, no further species-level consideration is employed in planning. Yet how responsible officials will be held accountable for such decisions is unclear. The burden of proof for determining the effectiveness of the coarse-filter approach is not addressed. These species-specific requirements represent the USFS commitment to the fine-filter approach in section 219.9.

Notably, the new rule eliminates the requirement for maintaining viable wildlife populations, in contrast to the 1982 rule's viability provision for vertebrates and the provisions of the 2000 rule that would have extended the requirement to other species. Since the agency only commits to maintaining the viability of species of conservation concern, under the 2012 rule the USFS has no obligation to address the decline of any species not listed, proposed, or a candidate under the ESA, unless the responsible official, in this case the Regional Forester, expresses substantial concern about its persistence. Thus, any number of species could pass from secure to endangered status before any federal intervention would be required. However, in contrast to the 1982 rule, the agency can commit to maintaining viable populations of non-vertebrates by identifying them as species of conservation concern.

Historically, the diversity provisions of the NFMA have been one of the most controversial aspects of the planning rule, and the issue of how the USFS should address the clearly established public values associated with wildlife conservation often has been overshadowed by legal and technical arguments about the practicality of specific approaches to viability assessment. For example, over the course of the drafting and judicial review of multiple rules, considerable disagreement existed as to whether a requirement to maintain viable populations of all species, or just vertebrate species, or just at-risk species was an attainable goal. Understandably, the USFS has been reluctant to commit the agency to a species viability standard with which demonstrating compliance is difficult. At any point in time, all species have some non-zero probability of extinction; thus, viability can never be guaranteed. Viability is a probabilistic concept that invokes a specific level of risk over a stated time horizon, and proponents of the viability standard have had difficulty explaining to the public—and sometimes to their colleagues in wildlife management—how probabilistic events can be addressed in legally enforceable standards.

Nonetheless, in its 2012 record of decision, the agency commits to maintaining the viability of species of conservation concern, arguing that the combination of coarse- and fine-filter approaches it proposes are scientifically defensible, will adequately protect biodiversity on its lands, and will not be too costly to implement (77 FR 21162). However, the planning rule does not specify how viability will be assessed or what information will be used to assess a species' viability. Additionally, species identified as being of conservation concern could experience sharp range restrictions, since the regulations no longer require viable populations to be well-distributed, as was the case under the 1982 rule. Instead, the new rule defines of a viable population as one that "continues to persist over the long term with sufficient distribution to be resilient and adaptable to stressors and likely future events" (36 CFR §219.19 [2012]).

Finally, the USFS may absolve itself of responsibility for species-level conservation if the agency determines that maintaining a viable population of a species of conservation concern is beyond the capability of the plan area. In this case, which might result from stressors extrinsic to the planning area, such as climate change or the loss of habitat in other regions, the responsible official is required to document the basis for that decision and include plan components that contribute to the maintenance of a viable population across multiple land ownerships, in coordination with other managers and private parties working across jurisdictional boundaries, to the extent practicable.

Monitoring

Monitoring requirements are outlined in section 219.12. The planning rule requires a monitoring program for each National Forest, which can be developed jointly across forests and must be developed in coordination with the Regional Forester and the Research and State & Private branches of the agency. Plan monitoring programs must include questions and indicators; for diversity, these include indicators addressing the status of ecological conditions and the status of focal species, defined in the rule as "a small subset of species whose status permits inference to the integrity of the larger ecological system to which it belongs and provides meaningful information regarding the effectiveness of the plan in maintaining or restoring the ecological conditions to maintain the diversity of plant and animal communities in the plan area. Focal species would be commonly selected on the basis of their functional role in ecosystems" (36 CFR § 219.19 [2012]). Regional Foresters are to develop "broader-scale monitoring" for questions that are relevant at scales larger than the planning area. In all cases, monitoring information is to be compiled, evaluated, made available to the public, and used to inform adaptive management of the plan area. Thus, the new rule adopts, for the first time, a multi-scaled approach for monitoring and codifies the intent, although not the process, for implementing a transparent and data-driven approach to adaptive management. Although the adoption of a focal species approach based on functional roles in sustaining ecosystem processes reflects the logic of the 2000 rule, the 2012 rule draws no connection between the monitoring of focal species and the conservation of their roles in the ecosystem. The new rule does not include a requirement to maintain the viability of focal species, despite the fact that it is the status of these species that is meant to indicate whether the USFS is successfully maintaining and restoring ecosystem diversity and integrity. Additionally, the 2012 rule does not provide a requirement to monitor species of conservation concern, despite their established vulnerability to local extirpation. Consequently, the fine-filter approach to monitoring is explicitly separated from the fine-filter approach for biodiversity conservation.

Alternatives Not Selected

Although a review of the key provisions of the planning rule provides direct insight into the place of wildlife conservation in the future of forest planning and management, examination of the alternatives not selected reveals the underlying logic, pivotal choices, and philosophical foundations of the Forest Service's interpretation of the NFMA and reconceptualization of its institutional role and responsibilities to the public. The USFS considered several other alternatives in its Programmatic Environmental Impact Statement, in addition to the selected alternative (i.e., the final rule), which was a modified version of Alternative A. Alternative B closely followed the 1982 rule, notably in regards to the viability provision (". . . fish and wildlife habitat shall be managed to maintain viable populations of existing native and desired non-native vertebrate species in the planning area . . ." [36 CFR 219.19]). The agency provides a lengthy rationale for not selecting Alternative B, focusing on the defects of the 1982 viability provision (see 77 FR 21162:21168). This rationale also pertains to the selection of the final rule (modified Alternative A), which dropped the 1982 viability provision with the exception of "species of conservation concern" (see below). The agency states the 1982 rule "included planning procedures that do not reflect current science or result in unrealistic or unattainable expectations because of circumstances outside of the Agency's control, particularly for maintaining the diversity of plant and animal species" (77 FR 21162:21169). The USFS further justifies dropping the requirement to maintain species viability by stating, "[T]here are limitations on the Agency's authority and the inherent capability of the land" (77 FR 21162:21169). It notes that forest clearing in South America and habitat fragmentation in the Rocky Mountains on private land affect the agency's ability to maintain viable populations on National Forest System lands. For reasons such as these, the agency notes, the USFS cannot ensure a species' existence in the planning area when circumstances outside of its control may be contributing to population declines. It also notes that managing for the habitat of a single species sometimes impinges on management requirements for a species listed under the

ESA, or on other necessary activities the agency must undertake to comply with statutory requirements. Furthermore, the agency writes, some forests simply cannot support viable populations of species that are rare and far-ranging, like wolverines (*Gulo gulo*), and require more habitat than is available on a single National Forest unit.

Alternative C included no specific provisions for biodiversity conservation beyond the minimum requirements of the NFMA. This alternative was highly discretionary, leaving decisions about the requirements for assessment, planning, and monitoring to the USFS Directives' System (i.e., the agency's handbook and manual), whose provisions are not legally binding. The high degree of discretion in this alternative, according to the agency, would have resulted in too much variation in implementation: "There would be no certainty with regard to the inclusion of any plan components beyond the minimum required by this Alternative, and a potential lack of consistency across the National Forest System" (77 FR 21162:21170).

Alternative D "was designed to evaluate additional protections for watersheds and an alternative approach to addressing the diversity of plant and animal communities" (77 FR 21162:21170). This alternative required watershed-scale assessments of climate change vulnerability and designation of key watersheds to anchor the assessment and maintenance of the ecological status of aquatic, riparian, and terrestrial components of watersheds (USFS 2012). Establishing connectivity between habitats and discrete populations of species would also have been required. The alternative maintained and extended the 1982 viability requirement, stating the National Forests would provide for viable populations of native and desired non-native species in each planning area. The USFS was required to use the best available science to determine ecological conditions necessary to support viable populations, as informed by the "current and likely future viability of focal species within the planning area" (USFS 2012:F-9). To address the agency's concern that it cannot ensure the viability of populations on its lands, Alternative D included language that required the Secretary of Agriculture to provide notice to the public and allow for public comment if the agency determined it could not provide for viable populations of native or desired non-native species in a plan area. Furthermore, the agency was required to provide for viability of such a population to the maximum extent practicable and to take no actions that would increase the likelihood of extirpation of a population in the planning area. As with the selected alternative, Alternative D required monitoring of the status and trends of focal species, but with the additional requirement that triggers be identified for focal species' monitoring that would initiate a review of planning and management decisions to achieve compliance with the viability standard. This alternative explicitly stated that population surveys of focal species would be conducted using presence–absence data, occupancy modeling, genetic monitoring, or count-based methods. Alternative D was not selected because of the high anticipated planning and monitoring costs (77 FR 21162). The record of decision states that many plans already incorporate elements of this alternative, but that it is too prescriptive to allow for efficient, effective, and flexible management of all National Forests (77 FR 21162).

Finally, Alternative E was highly prescriptive in terms of requirements for public notification, assessment, and monitoring. It would have required specific monitoring questions, indicators, and triggers for changes in management action. The diversity requirements would have been similar to those in the selected alternative, but with more emphasis on monitoring of species' status and trends. The alternative was rejected for the same reasons as Alternative D.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS FOR IMPLEMENTING THE 2012 PLANNING RULE

In theory, the new planning rule could be implemented in a robust way, drawing on the best available science to protect plant and animal diversity on National Forest System lands. However, the primary change introduced by the 2012 rule is the considerable discretion afforded centralized authorities, particularly at the regional level, in how general provisions will be implemented. Based on the management history of the USFS, numerous aspects of the 2012 planning rule are of concern, primarily because they defer many fundamental details to the interpretation of officials who may lack scientific background and disciplinary depth in wildlife biology and may have disincentives to prioritize wildlife. A number of scientists and scientific societies (including The Wildlife Society) commented on the draft rule and noted that it leaves more decisions about diversity conservation to agency discretion than did the 1982 rule. Forest Service officials must strike a fine balance between prescriptive standards and discretion or flexibility in a rule that is meant to guide planning years into the future on the entire National Forest System. Although some discretion is necessary, a rule must be sufficiently prescriptive to ensure that the National Forests do not implement a loosely written and unenforceable standard with so much variability across management units as to compromise the conservation of biological diversity.

Discretion, Authority, and Responsibility in Wildlife Conservation

Highly discretionary mandates are especially problematic for protecting resources such as wildlife that, without clear substantive requirements, have historically received less attention in land management. The 1897 Organic Act gives the USFS wide discretion by providing an open-ended mandate to secure water flows and provide timber. The Multiple Use Sustained Yield Act (MUSYA), passed in 1960, expanded the factors that the USFS must consider in planning, including wildlife conservation. However, the language in the MUSYA does not require the USFS to conserve wildlife in any specific fashion, only to consider the wildlife resource when planning for multiple-use. The concept of multiple-use, according to the courts, "breathes discretion at every pore" (*Perkins v. Bergland* 1979). Wildlife never gained serious consideration in forest management under the MUSYA, in part because of the agency's deference to state wildlife agencies, which have generally focused on game species and sport fisheries.

We have consistently heard many USFS personnel argue that their primary responsibility is to manage the habitat on USFS lands, whereas actual populations are the domain of the states. However, the USFS clearly has the power to manage wildlife on its lands. The United States Constitution's Property Clause (Art IV, section 3) gives Congress proprietary and sovereign powers over its property, and it may delegate decisions regarding federal lands to executive agencies. The Supreme Court has repeatedly observed that this power over federal land is "without limitations" (*United States v. San Francisco* 1940). The Court's expansive reading of the Property Clause also extends to managing wildlife on federal lands. The dispositive case is *Kleppe v. New Mexico* (1976), where the Court states, "the 'complete power' that Congress has over public lands necessarily includes the power to regulate and protect the wildlife living there" (426 U.S. 529: 541). Of course, the states also manage wildlife on federal lands, but as made clear in *Kleppe*, "those powers exist only in so far as [their] exercise may be not incompatible with, or restrained by, the rights conveyed to the Federal government by the Constitution." (426 U.S. 529: 545). Though the USFS seldom chooses to assert its full wildlife management powers, the Courts continue to emphasize the Property Clause's application to wildlife (see, e.g., *Wyoming v. United States* 2002).

Concerns about wildlife were one of the central factors precipitating the passage of the NFMA in 1976, and the USFS has a clear responsibility under the Act to manage for biodiversity. The Act's legislative history shows that its diversity provision was meant to require "Forest Service planners to treat the wildlife resource as a controlling, co-equal factor in forest management and, in particular, as a substantive limitation on timber production" (Wilkinson and Anderson 1987:296). When the NFMA was passed, it included language stating that the USFS has a responsibility to be "a leader in assuring that the Nation maintains a natural resource conservation posture that will meet the requirements of our people in perpetuity" (16 U.S.C. §1600[6]) and an explicit requirement to protect plant and animal diversity. To ensure that the agency's new requirements were effectively translated into administrative regulations, Congress required the agency to convene a Committee of Scientists to inform the writing of these regulations, which were finalized in 1982 (16 U.S.C. §1604[h][1]).

Timber harvest on the National Forests, nonetheless, continued to increase steadily, until the late 1980s. At that time, citizen enforcement, frequently manifest through appeals and litigation based on substantive provisions like the 1982 rule's viability standard and the ESA, was a major factor that led to significant declines in timber production (from >13 million board feet/year in the late 1980s to <2 million in the early 2000s). Legal exposure created by the suite of substantive requirements to protect biological diversity under the NFMA and ESA forced the agency to address wildlife conservation, something that had not come to pass under the MUSYA. However, even in the 1990s, pressure to prioritize timber production over the protection of wildlife remained strong because of internal biases, financial incentives, and Congressional intervention (Wilkinson 1992, Government Accountability Office 1997, Corbin 1999).

Although agency culture and priorities have shifted over time, biodiversity conservation still may conflict with activities like timber harvest, fuels reduction, recreation, or energy development, all of which the USFS has strong economic and political incentives to promote. Literature in political science and economics predicts that when given conflicting tasks by Congress, such as the multiple use mandate, agencies systematically prioritize high incentive and measurable goals over those that are lower incentive and more difficult to measure (Biber 2009). A highly discretionary NFMA diversity regulation could lead the USFS to prioritize higher incentive and measurable goals that are supported by political interests.

Given this reality, even when regulations for protecting plant and animal diversity are well meaning and scientifically sound, if they are not specific, measurable, binding, and enforceable, history suggests that effective wildlife conservation planning will end up as a secondary objective (Houck 1997). Specific, mandatory language is needed to protect wildlife on the National Forests, a point not lost on the first Committee of Scientists, who wrote the following in 1979, "It is simply not possible to carry out the planning requirements of NFMA in accordance with a set of regulations that contain nothing but generalities" (44 FR 53967: 53968). Such specificity, said the Committee, is what the NFMA requires. Historically, the NFMA's diversity provision and its associated regulations have provided an effective counterbalance to competing agency demands and political pressures. However, without more specific requirements, the administrative discretion in the 2012 rule's diversity provisions will lead to varied implementation across management units, give managers who are not committed to wildlife conservation the leeway to pursue other management goals without concern for biodiversity, and leave managers who are committed to protecting biodiversity without a solid, legal framework to help them withstand internal and external pressures to prioritize other factors.

Although the diversity provisions in the 2012 planning rule itself are highly discretionary, the agency, through the Directives system, could adopt standards and practices for wildlife conservation that are more prescriptive and would help to ensure that the rule is implemented in a more robust fashion and informed by the best available science. We urge the agency to implement the rule in a manner that closes the gap between the stated purpose of maintaining ecological integrity and diversity, and the highly general and discretionary operational provisions in the rule that are meant to achieve these purposes. The Wildlife Society and other professional organizations can play an important role in guiding this process, and for this purpose, we offer a series of recommendations that would strengthen the key wildlife provisions in the 2012 rule.

Coarse-Filter Contributions

Coarse-filter approaches, typically focused at broader spatial scales than fine-filter strategies, are aimed at communities, ecosystems, or landscapes (Schwartz 1999). Their central role in the 2012 rule complements fine-filter provisions and commits the USFS to multi-scaled assessment and monitoring efforts. Coarse-filter conservation strategies often rely on habitat predictors (e.g., dominant vegetation and landform) derived from satellite imagery (e.g., the California Wildlife Habitat Relationships System, http://www.dfa.ca.gov/biogeodata/cwhr). Under this approach, all appropriate habitats within a planning unit that intersect the species' geographic range are typically assumed to support the species. This assumption is often based on anecdotal occurrence data because the spatial extent of coarse-filter strategies often constrains the agency's ability to implement probability-based survey designs. The consequence is that commission errors are likely, which can lead to the erroneous conclusion that animal diversity is being maintained when it is not. Although these concerns limit the ability the coarse-filter approach to serve as a substitute for fine-filter assessments, a management objective to sustain dominant vegetation communities and their successional stages at broad spatial scales is an essential aspect of a comprehensive approach for sustaining biological diversity. In the context of the diversity requirements of the 2012 rule, measures of the effectiveness of the coarse-filter are presented in terms of species' metrics (e.g., number of rare and imperiled species conserved, presence of apex consumers, species richness, etc.). Therefore, verifying the efficacy of the coarse-filter approach requires some level of direct species-level assessment, and a comprehensive diversity policy requires a carefully balanced coarse-filter/fine-filter strategy.

Implementing the Fine-Filter Approach

We are concerned with the limited commitment to conduct fine-filter (species-level) assessments in the new rule. We found little scientific evidence to suggest that maintaining the diversity and integrity of a combination of habitat types "will provide the ecological conditions for the long-term persistence of most species within the plan area" (36 CFR §219.9). The Committee of Scientists stated, "Habitat alone cannot be used to predict wildlife populations" and "diversity is sustained only when individual species persist; the goals of ensuring viability and providing for diversity are inseparable" (Committee of Scientists 1999, Chapter 3:19,38). For this reason, the fine-filter species assessment is critical.

The rule is inaccurate in the way it portrays its coarse- and fine-filter approaches. It claims that the coarse-filter approach, along with the inclusion of fine-scale habitat management requirements for species that are not adequately protected, constitutes a combined coarse-filter/fine-filter approach. This discussion misconstrues fine-filter species conservation approaches, which entail direct assessment at the species level, including monitoring state variables such as a species' abundance, density, survival, birth rate, or occupancy. Managing fine-scale habitat components for a given species is not the same as fine-filter assessment.

The USFS defines focal species, in part, based on their functional significance to ecosystem processes (36 CFR §219.19[2012]). The planning rule requires the selection and monitoring of focal species "to assess the ecological conditions required under §219.9 . . ." (§219.12[a][5][iii]), and it is this aspect of the rule that holds the most promise as a genuine, complimentary fine-filter approach to wildlife conservation planning. The USFS defines ecological conditions as "the biological and physical environment that can affect the diversity of plant and animal communities, the persistence of native species, and the productive capacity of ecological systems" (36 CFR §219.19[2012]). An emphasis on monitoring species with known or suspected functional significance to ecosystems process and sustainability is appropriate. Ecosystem resilience is strongly related to native species diversity and functional redundancy (the degree to which multiple species perform similar ecosystem functions [Naeem et al. 2009]). In general, ecosystems with greater native species diversity are more resistant to disturbance, recover more quickly following disturbance, and are less likely to experience irreversible changes than species-poor communities (Cottingham et al. 2001, Hooper et al., 2005, Naeem et al. 2009). Furthermore, species loss ranks among the most severe global change stressors, with effects comparable to those of climate warming, acidification, and elevated carbon dioxide (Hooper et al. 2012). Therefore, it is inconsistent with the stated intent of §219.9 to maintain or restore ecological conditions not to include a commensurate requirement to maintain viable populations of focal species.

Another central requirement of the 2012 rule is the mandate to contribute to the recovery of proposed, candidate, and listed ESA species and to protect viable populations of species of conservation concern. Section 219.9 requires that species-specific habitat management components be built into plans if the responsible official determines that coarse-filter approaches are insufficient for maintaining viable populations of species of conservation concern, and ESA species, within the plan area. We are concerned that, as presently construed, the rule does not require the monitoring of these species. Thus, it is unclear what information will be used to determine if a species maintains a viable population within the plan area, or if it requires additional species-specific conservation actions. Because the coarse-filter approach may be insufficient to provide insights into the status and trend of species (Cushman et al. 2008), some direct species-level monitoring is necessary. Without such monitoring, the USFS's approach is problematic; by the time evidence of further decline for these already at-risk species is found, threats may have significantly increased.

Ideally, the rule would have committed to population-level monitoring and viability for both focal species and species of conservation concern. Extending the viability requirement to focal species, selected in part because of their known or suspected functional significance, is a logical way to address the ecosystem integrity goals of the rule. Further, monitoring species of conservation concern will provide essential information to assess their viability. These changes, incorporated into the Directives, would connect the commitment to species-level conservation with the mandate for adaptive management and bring greater cohesion to the disjointed diversity provisions in the 2012 rule. In addition, all species-level monitoring should include trigger points so that significant declines in either focal species or species of conservation concern would initiate reviews of management policies.

Selecting Species of Conservation Concern and Focal Species

The process for selecting focal species and identifying species of conservation concern, separately or in concert, is not detailed in the rule. The rule simply states that the selection of species of conservation concern will be based on the best available science and evidence of substantial concern about their long-term persistence in the plan area. The Record of Decision indicates that further guidance will be provided in the Directives, but that the Department of Agriculture expects species to be identified based on existing classifications of risk, such as NatureServe conservation status or those listed as threatened or endangered under state law (77 FR 21162:21218). In addition to referencing NatureServe and state law, we recommend the agency also consider IUCN red-list species that are not already listed under the ESA, and high priority species identified in State Wildlife Action Plans; if such species are not selected, a rationale for failing to designate them as species of conservation concern should be required.

Criteria for focal species selection include the species' functional roles in the ecosystem and sensitivity to changing conditions, management activities, particular threats, or desired ecological conditions (77 FR 21162). This is consistent with recommendations of the most recent Committee of Scientists' Report (Committee of Scientists 1999). Additional guidance in the Directives will be necessary to establish and maintain consistency and efficacy across management units in the selection of focal species. Noon et al. (2009) provide useful guidance on focal species selection for fine-filter assessments on federal public lands. Furthermore, we see no reason that species identified as species of conservation concern cannot also be identified as focal species, providing a ready avenue for conceptual integration of the fine-filter approaches under the new planning rule.

Establishing a step-down process to identify and prioritize species for fine-filter monitoring that reflects the reality of Forest Service monitoring budgets remains a major challenge. This topic goes beyond the scope of our paper, but to initiate discussion, we suggest that identifying the core species (Magurran and Henderson 2003) that are 1) persistent members of a given management unit; 2) functionally significant; and 3) at risk in that unit may be a first step in developing a manageable species set.

Developing Informative Monitoring Programs

The planning rule requires forests to develop monitoring programs that will include a set of questions and indicators to track change, measure management effectiveness, and assess progress towards desired future conditions. The rule only commits to monitoring focal species, which as mentioned above, may include species of conservation concern (the fine-filter approach). It also requires monitoring a select set of ecological conditions in accordance with the objectives of §219.9 (the coarse-filter approach). The Regional Forester is required to develop a broad-scale monitoring plan to address issues relevant at a scale larger than a single National Forest. The content of the broad-scale monitoring plan is at the discretion of the Regional Forester, and s/he is required to coordinate with other jurisdictions, other branches of the USFS, and the public. Additionally, monitoring plans may be coordinated across units. The responsible officials are to conduct biennial evaluations of monitoring information and adjust management activities as necessary.

At the outset, the discussion of species monitoring in the Record of Decision (77 FR 21162:21232–21233) is confusing and suggests a critical misunderstanding by the USFS of environmental monitoring. The Record of Decision (77 FR 21162:21233) states, "The final rule does not require monitoring species population trends. Species population trend monitoring is costly, time intensive, and may not provide conclusive or relevant information." This perspective is at odds with the general understanding in the scientific literature of environmental monitoring. For example, Suter (1993:505) states that monitoring is the "measurement of environmental characteristics over an extended period of time to determine status or trends in some aspect of environmental quality." Monitoring of an appropriate state variable (e.g., occupancy) is conducted at regular intervals to assess both the current state and time trend in some ecological resource (e.g., a species' population [Noon 2003, Nichols and Williams 2006])—that is, the stated purpose of monitoring is to estimate temporal trends.

Provisions in the rule encourage the development of robust monitoring strategies. However, our primary concern is whether these strategies will be developed, funded, implemented, and designed in such a way that they inform adaptive planning. As noted previously, monitoring has been chronically underfunded by federal agencies. The rule requires development of a monitoring plan but does not specify a particular standard of quality or utility of monitoring data. Since Congress annually sets the agency's budget, the USFS cannot commit to funding monitoring at a particular dollar amount. However, committing a certain percentage of planning dollars to monitoring may be possible so that the USFS can address its commitment to adaptive management.

Following the United States Supreme Court's decision in *Norton v. SUWA* (2004), enforcing monitoring requirements of federal land use plans is difficult. In language easily extendible to NFMA plans, that case held that commitments to monitor in Bureau of Land Management land use plans are not generally binding or reviewable under the parameters of administrative law. The Court noted that monitoring requirements could perhaps be written in such a way as to make them enforceable, if they were written as clear and binding commitments. In some cases, when monitoring activities are clearly required before undertaking certain activities, monitoring can be enforceable in court (Blumm and Bosse 2007). However, because requiring or enforcing funding levels or data quality standards for monitoring programs is generally difficult, oversight will be necessary to ensure that monitoring occurs in a way that it clearly assesses management and restoration actions.

We recommend that multi-party oversight boards be established to aid in the design of monitoring programs, contribute to the selection and prioritization of monitoring state variables, provide science consistency checks, provide interpretations of the monitoring data, suggest when changes to management practices are needed, and advocate for consistent funding. Because monitoring data will unlikely be subject to judicial review, oversight from a multi-party stakeholder monitoring board could increase the likelihood that monitoring will provide reliable information and useful insights into future decision making (Nie and Schultz 2012). Such boards must consider how monitoring data will inform decision making and the level of statistical certainty required to trigger a change in management actions.

All species-level monitoring should include trigger points so that significant declines in either focal species or species of conservation concern will initiate reviews of management policies. If trigger points are not identified, monitoring data may not feed back into adaptive planning and decision making (Noon 2003). Triggers will be critical for species-level monitoring and for any evaluation of species viability. Monitoring enforceability also would be substantially increased if forest plans included requirements that before approving any major projects, such as those requiring an Environmental Impact Statement, the responsible official find that monitoring programs are being implemented and that no trigger points have been exceeded without corrective action.

Maintaining Current Populations and Adequate Distribution of Species

Whether the planning rule intentionally allows for local extirpation of species or range reductions in cases where this might be avoided is unclear, but the decline and loss of species from the planning area is an allowable outcome of USFS management under the new rule. Aside from the loss of a broader viability requirement, this is the most significant change from the 1982 rule: the replacement of language requiring that viable populations be well-distributed, with the definition of a viable population as one that "continues to persist over the long term with sufficient distribution to be resilient and adaptable to stressors and likely future events" (36 CFR §219.19 [2012]). The impact of the change stems from the fact that what constitutes a "sufficient distribution" is not defined in the rule, providing broad discretion to the responsible official and obfuscating the well-established relationship between geographic distribution and persistence likelihood (e.g., Harris and Pimm 2008).

Furthermore, the rule establishes that the USFS does not need to protect viable populations, as required in the 1982 rule, if this is not within the "inherent capability of the plan area," a vague concept that is never defined in measurable terms. In this case, the USFS is held to a much lower conservation standard: documenting the rationale for such a determination and working across land ownerships to create management standards and guidelines to maintain or restore conditions that will contribute to maintaining a viable population of the species within its range (36 C.F.R. §219.9(b)(2)(i) [2012]). The USFS also states, "the individuals of a species of conservation concern that exist in the plan area will be considered to be members of one population of that species" (77 FR 21162:21217). In light of this, whether the agency is committing to maintaining a viable population of a species of conservation concern when it is not within the inherent capability of a single plan area to protect a viable population is not entirely clear. Depending on how the agency interprets these standards, it might never have to commit to maintaining a viable population of a low-density, wide-ranging species, but it might have to commit to maintaining multiple viable populations of species with more constricted ranges.

To address ambiguities in the 2012 viability requirements, we recommend that the USFS explicitly recognize the importance of maintaining a wide geographic distribution for species viability. Species that are widely distributed across the landscape are much less likely to experience spatially correlated disturbance events (den Boer 1981). Maintaining the distribution and viability of rare or widely distributed species and populations will require close coordination among administrative units. Guidance should be included in the Directives indicating that the agency should assess viability (perhaps employing more efficient distributional analyses based on occupancy [Noon et al. 2012]) across ownerships and plan units, when this will enhance the likelihood of persistence for individual species. When the USFS determines that maintaining a viable population of a species is not within the inherent capability of the plan area, the agency should solicit scientific comment and review. This review will help ensure that the agency is aware of all relevant scientific information that may conflict with their determination and will better prepare the agency to defend its decisions against possible legal challenge. In cases where the USFS determines that providing for a viable population of a species that relies upon National Forest System lands for its habitat is not within the capability of the plan area, we recommend that the agency task itself with restoring populations, to the maximum extent practicable. At the least, a standard should be included in the Directives that directs the agency not to authorize or permit activities that reduce the viability of any species of conservation concern.

Development on private land and other activities external to National Forest System lands may affect species such that the USFS cannot alone ensure their viability. A critical question is to what extent should this compel the USFS to compensate for declines in species status due to factors outside of their control. Recall that the NFMA emphasizes the National Forests' role in conserving resources for the American people, in perpetuity. It does not imply that this objective is restricted to National Forest System lands. There is ample historical precedent for the USFS to consider what is happening outside of its jurisdiction and proactively respond on the National Forests (Nie and Miller 2010). In the view of the first chief of the USFS, Gifford Pinchot, 1 rationale for establishment of the National Forests was to compensate for unsustainable management of resources on private lands (Wilkinson 1992). Pinchot was focused on unsustainable timber harvest at the time, but the reasoning applies widely to other natural resources on USFS lands based on changing public values and priorities. The USFS, in its 2012 rule, emphasizes its responsibility to maintain and restore ecosystem diversity and integrity, and diverse plant and animal communities are fundamental to ecosystem integrity (Naeem et al. 2009). If development on private land is adversely affecting biodiversity, the USFS has a greater, not lesser, responsibility to protect species on its lands. This compensation principle will become even more significant given predictions of private land development in the future, with much of this development projected in the wildland urban interface (Nie and Miller 2010). The National Forests, and federal lands in general, will become more important to wildlife in increasingly developed landscapes. Therefore, the "inherent capacity" clause of the 2012 rule should be used rarely, if at all, and if used, be subject to scientific and public review. The USFS must recognize its increasingly important mission to conserve the nation's forest and grassland ecosystems during the current period of rapid global change and species loss, when unpredictable transformations of ecosystems may be the "new normal" (Barnosky et al. 2012).

Considerations Regarding the Relationship Between the NFMA and the ESA

Important intersections exist between biodiversity conservation requirements under the NFMA and the ESA, which work together as part of this nation's biodiversity conservation policy. Wildlife provisions in forest plans are a significant factor in ESA decision making (see below), and ESA decisions have profound and far-reaching implications for forest management. Ideally, viability protection on National Forests would serve as an early warning signal that a species may be heading towards local extirpation or extinction. A proactive approach to address risks to a species' viability could avoid costly and polarizing ESA decisions that might limit management flexibility for the USFS.

On the National Forests, currently 430 species are listed under the ESA as threatened or endangered, and an additional 60 species are candidates for listing (USFS 2011:14). More than 647,000 ha of terrestrial habitat and 35,000 km of stream habitat on USFS lands are designated as critical habitat under the ESA (USFS 2011:14). For these and other reasons, the 2012 planning rule emphasizes the connections between forest planning and the ESA more than previous regulations:

> The [Department of Agriculture] anticipates that plan components, including standards or guidelines, for the plan area would address conservation measures and actions identified in recovery plans relevant to T&E [threatened and endangered] species. When implemented over time, these requirements would be expected to result in plans that will be proactive in the recovery and conservation of the threatened, endangered, proposed, and candidate species in the plan areas. These requirements will further the purposes of section 7(a)(1) of the ESA, by actively contributing to threatened and endangered species recovery and maintaining or restoring the ecosystems upon which they depend (77 FR 21162:21215).

One way in which the USFS can actively contribute to species conservation and recovery is by providing wildlife and habitat-based standards in individual National Forest plans. The NFMA requires the incorporation of standards and guidelines in land and resource management plans (16 U.S.C. 1694). Standards are mandatory constraints on USFS projects and activities and are used to achieve or maintain desired conditions and planning objectives, to avoid or mitigate undesirable environmental impacts, and to meet applicable legal requirements (76 FR 8480). Guidelines, as commonly applied, also constrain decision making but allow for some deviation from rules as long as the intent of the guideline is achieved (76 FR 8480).

The types of wildlife and habitat-based standards used in forest planning differ in scale, specificity, and complexity. Some standards cover multiple National Forests, such as the Northwest Forest Plan's Aquatic Conservation Strategy (discussed below) and the Inland Native Fish Strategy. The latter, covering at one point 22 National Forests, is used to protect native fish and their habitats in eastern Oregon and Washington, Idaho, western Montana, and portions of Nevada. It does so by using several riparian management objectives, standards, guidelines, and monitoring requirements (USFS 1995). The Inland Native Fish Strategy's standards and guidelines replaced conflicting direction in multiple National Forest plans, except when those forests provided for more protection for inland native fish habitat. Standards can also be applied forest-wide, such as requiring that all snags over a certain size be retained or that a specified percentage of old growth be maintained on a National Forest. Other standards apply to particular management areas or zones as delineated in a land use plan; they often permit or prohibit various uses, such as grazing or the application of herbicides in a municipal watershed zone.

An enduring debate continues over the appropriate role of standards in forest planning. The 2012 rule requires every plan to include standards as 1 of 5 plan components (36 C.F.R. §219.7), but it leaves their application to the discretion of the responsible official, with the expectation that further direction will be provided in the Directives system (77 FR 21162:21206). Regarding the diversity of plant and animal communities, the rule requires standards or guidelines be used "to maintain or restore ecological conditions within the plan area to contribute to maintaining a viable population of the species within its range" (36 C.F.R. §219.9). Standards for wildlife protections should play a significant role in the new forest plans that will be written under the 2012 regulations. Legally binding and enforceable standards promote accountability and provide increased certainty about future management actions. Without them, there is an increased risk that wildlife protections will give way to other agency pressures and priorities.

Forest plan standards can play significant roles in decisions to list or delist a species under the ESA. One of the 5 factors to be considered by the wildlife regulatory agencies that enforce the ESA (the National Oceanic and Atmospheric Agency [NOAA] Fisheries and the U.S. Fish and Wildlife Service [USFWS]) in making ESA listing decisions is "the inadequacy of existing regulatory mechanism[s]" (16 U.S.C. §1533). Vague, voluntary, speculative, and unenforceable measures found in plans are generally not considered a sufficient regulatory mechanism (*Oregon Natural Resources Council v. Daley* 1998). Instead, federal wildlife agencies and the courts typically assess whether a plan contains specific and legally enforceable standards having regulatory force. Forest plan standards also can be relevant for determinations made by the wildlife regulatory agencies under section 7 of the ESA, which requires federal agencies to undergo consultation with the wildlife agencies to ensure their projects will not cause jeopardy to a listed species.

Several cases have been decided in which NOAA Fisheries and the USFWS made a no-jeopardy determination under section 7 of the ESA or decided not to list a particular species because a forest plan contained binding standards and other regulatory mechanisms to protect the petitioned species. One example is the decision not to list the Queen Charlotte goshawk (*Accipiter gentilis laingi*) in southeast Alaska. Roughly 80% of this region is managed by the Tongass National Forest, and petitioners argued that old-growth logging in the region posed a threat to goshawks. Standards and other regulatory mechanisms specified in the 2007 Tongass Land Management Plan were significant factors in the decision by the USFWS to not list the goshawk (72 FR 63133). The USFWS also emphasized the legally binding and enforceable nature of Tongass forest planning standards in its 1997 status review of the species (USFWS 2007), and the Department of the Interior asked the USFS to retain the Conservation Strategy in the 2008 Tongass Forest Plan Amendment. The USFS also recognizes the significance of these wildlife standards. Possible changes to the Strategy, according to Undersecretary of Agriculture Harris Sherman, "could hamper the plan's ability to maintain viable populations of plant and wildlife species [and] this could lead to the need for USFWS to reconsider its previous determinations regarding the goshawk . . ." (Sherman 2011:8).

The Aquatic Conservation Strategy, part of the Northwest Forest Plan, provides another example of the interactions between binding standards and the ESA (USFS and Bureau of Land Management 1994). The purpose of the Aquatic Conservation Strategy is to maintain and restore the ecological health of watersheds in the northwestern National Forests. The Strategy includes several binding standards and guidelines that apply to key watersheds, riparian reserves, required watershed analyses, and watershed restoration. In biological opinions written in accordance with section 7 of the ESA, NOAA Fisheries equates Aquatic Conservation Strategy consistency with no-jeopardy findings, a practice that has satisfied the courts (*Pacific Coast Federation of Fishermen's Associations v. National Marine Fisheries Service* 2001). Standards such as these can be used to protect wildlife while also achieving the restoration and watershed protection purposes of the 2012 rule.

The lack of enforceable standards and clear conservation commitments made in forest plans also has been a factor influencing decisions to list a species. In these cases, NOAA Fisheries and the USFWS determine that a forest plan fails to provide sufficiently certain, binding, and detailed protection to a species to count as an adequate regulatory mechanism. One of the most significant decisions in this regard is provided by the listing of Canada lynx (*Lynx canadensis*) as threatened in 2000 (65 FR 16052). The species was classified as a sensitive species by the USFS before listing, but most National Forests with lynx did not have population viability objectives or management standards and guidelines in place at the time (63 FR 37005). The fact that forest plans in effect at the time did not provide enough protection and guidance for the conservation of the lynx is a primary reason why the species was listed. The USFWS determined that these forest plans permitted several actions that cumulatively could cause a significant threat to lynx persistence across its range (63 FR 37005). The USFS responded to the listing by amending multiple national forest plans to incorporate various lynx standards and guidelines (USFS 2007). Currently, the USFS does not have to engage in ESA consultation with the USFWS on a project-by-project basis if these projects comply with these binding and enforceable lynx standards. Another prominent example is the 2010 decision to list the greater sage-grouse (*Centrocercus urophasianus*) as warranted-but-precluded, meaning the species is warranted for listing but precluded from actually being listed because of funding limitations (75 FR 13910). The USFS manages roughly 8% of the sagebrush habitat significant to the species. Greater sage-grouse were designated by the USFS as a sensitive species on USFS lands across the range of the species, and 14 of these forests designated the bird as a management indicator species (75 FR 13910:13979). But of the 33 National Forests managing greater sage-grouse habitat, "16 do not specifically address sage-grouse management or conservation in their Forest Plans, and only 6 provide a high level of detail specific to sage-grouse management" (75 FR 13910:13980). The lack of detailed protections and the variation among National Forest plans in the greater sage-grouse area was an important factor in making the warranted-but-precluded determination (75 FR 13910).

Enforceable wildlife standards and protections on the National Forests also play a role in delisting species from the ESA. One of the few species to be delisted under the ESA is the Robbin's cinquefoil (*Potentilla robbinsiana*), an endemic plant found in the White Mountains of New Hampshire, in areas managed exclusively by the White Mountain National Forest (67 FR 54968). The USFS was able to assist in the recovery of this species by restricting entry to particular areas of the National Forest, relocating trails, and entering into a Memorandum of Understanding with the USFWS. This Memorandum of Understanding included provisions related to habitat protection and monitoring, and it served as a long-term commitment by the USFS to conserve this plant, irrespective of its status and potential delisting under the ESA (USFS and USFWS 1994). The USFS regulations also prohibited removing, destroying or damaging plants that are classified as threatened, endangered, rare, or unique (36 C.F.R 261.9). All of these specific actions and commitments—the protective actions taken by the White Mountain National Forest, the plant regulations, and the Memorandum of Understanding—served as an adequate regulatory mechanism for delisting the species by the USFWS.

A more controversial example is the proposed delisting of the Yellowstone distinct population segment of grizzly bears (*Ursus arctos horribilis*). The lack of regulatory mechanisms to protect grizzly bear habitat on National Forest System lands was 1 reason why the species was listed in 1975 (40 FR 31734). A conservation strategy for the bear was written pursuant to its recovery plan to provide adequate regulatory mechanisms after the bear's delisting. The USFS amended 6 forest plans to incorporate the habitat standards and other provisions in the conservation strategy. The USFWS considers these standards to be adequate regulatory mechanisms for the purpose of delisting grizzly bears, but much of the debate and litigation over the delisting decision centers on the sufficiency of these standards. A district court found the delisting impermissible, partly because the amended forest plans contained discretionary and legally unenforceable guidelines, rather than binding standards, in the bear's primary conservation area (*Greater Yellowstone Coalition v. Servheen* 2009). The Ninth Circuit disagreed with the lower court on this matter and found the standards, as applied by the USFS within the primary conservation area, to be sufficient under the ESA because they are a legally enforceable part of National Forest plans, and management of these forests must be consistent with their governing forest plans (*Greater Yellowstone Coalition v. Servheen* 2011).

The 2012 rule also requires that forest plans provide the ecological conditions to "contribute to the recovery" of listed threatened and endangered (T&E) species (77 FR 21162:21215, 36 C.F.R. §219.9). The USFS has an expectation that forest plans would use standards or guidelines "to address conservation measures and actions identified in recovery plans relevant to T&E species" (77 FR 21162:21215). Better use of ESA recovery objectives could lead to more proactive, integrated, and strategically coordinated forest plans.

We recommend that more guidance be provided as to how synergies might be developed between forest and ESA recovery planning. Scott et al. (2005:386) show that "most listed species will require continuous management action in order to maintain their recovered status." These "conservation-reliant species" can only be maintained as a self-sustaining population in the wild "if ongoing management actions of proven effectiveness are implemented" (Scott et al. 2005:386). The Memorandum of Understanding and revised forest plan for Robbin's cinquefoil provide this sort of ongoing protection to a conservation-reliant species, and similar standards in forest plans could do the same for other T&E species on the National Forests.

The number of ESA listing decisions will only increase in the future, given the September 2011 settlement between the USFWS and environmental groups requiring the agency to make listing decisions on over 800 species, including 262 candidate species, for which such decisions have been delayed (Center for Biological Diversity 2012). Altogether, another 1,000 listing decisions will possibly have to be made by 2020 (Rylander 2012:10018). Furthermore, conservation scientists, the IUCN, and the Intergovernmental Panel of Climate Change all predict increases in the number of species threatened with extinction (Scott et al. 2010). For these reasons, the impact of ESA listing decisions on National Forest management is likely to increase over time. The use of binding standards in forest plans would likely serve to decrease the number of species listed as threatened and endangered and promote delisting decisions in the future.

If implemented in a robust fashion, the NFMA's diversity mandate will serve as a precautionary and proactive approach to wildlife conservation. In contrast, the ESA provides a more reactive and crisis-based approach to decision making, since the law's protective measures are usually not initiated until a jeopardized species is listed, and by that time, it is already in the proverbial emergency room. Federal wildlife agencies take an average of 11 years to list species (Greenwald et al. 2006), frequently after their long-term viability is in doubt (Wilcove et al., 1993, Neel et al. 2012, Rylander 2012). Waiting until a species is on the brink of extinction before taking protective measures creates unnecessary risks to a species and increases the controversies, costs, and restrictions associated with their recovery. Furthermore, funding is inadequate to meet the needs of species that are already listed, are candidates for listing, or have been petitioned for listing (Scott et al. 2010). Strong wildlife provisions under the NFMA could provide an earlier, proactive response to species declines, lessening the trend for more listings under the ESA. Allowing populations to decline towards listing is not good policy ecologically, politically, or economically. It will only reduce management flexibility for states, private citizens, and federal agencies and will further burden managers implementing the already underfunded ESA.

CONCLUSIONS

Given clear guidance in the Directives and sufficient funding, the 2012 planning rule has the potential to be a highly effective framework for wildlife conservation on National Forest System lands. It commits the Forest Service to a formal adaptive management process, adopts a landscape perspective as the primary context for forest planning, strives to find an appropriate balance between coarse- and fine-filter approaches to the assessment of biological diversity, and codifies the need to monitor focal species at multiple spatial scales. These are all significant advances that signal the Forest Service's commitment to a new planning rule that is responsive to the status and trends of ecological systems, as well as the expectations of the nation for the wise stewardship and conservation of public lands and resources.

Although we are confident that the rule can be implemented so as to effectively conserve wildlife populations, we are concerned about the ambiguity of the plan's diversity provisions and the level of discretion permitted when interpreting and implementing the plan's most fundamental actions: identifying focal species, monitoring status and trends, establishing triggers for adaptive management, and taking action to sustain viable populations. Effective implementation of the rule will require a commitment to direct monitoring of focal species, species of conservation concern, and ESA species, as well as a commitment to maintaining their viability. Without this commitment, the provision to sustain biological diversity is incoherent and unlikely to be effective. Triggers will have to be established for monitoring of species to signal when a review of management approaches is necessary. Without an assessment of the effects of management actions via monitoring, the agency cannot fulfill its obligation to manage adaptively. When private land development or other more distant factors affect the viability of species, the USFS should place more, not less, emphasis on providing for viable populations to the extent practicable. The design of monitoring programs, determinations about the inherent capability of the land, and selection of focal and species of conservation concern should be based on the best available scientific information.

The language of the new rule is more discretionary than the 1982 rule, and it removes the requirement to maintain viable populations of all vertebrate species. Although this is unquestionably a significant change in regulatory language, some might argue the 2012 rule merely codifies the way the USFS has managed for diversity since 1982. In practice, management indicator species seldom have been monitored directly in a way that allowed for a clear understanding of their response to management actions, and the USFS has been managing for Regional Forester Sensitive Species by relying primarily on habitat measurements as proxies for the species' current status. In effect, the 2012 rule simply makes it more explicit that this relaxation of the standards established in the 1982 rule will be the USFS's accepted standard for managing for diversity—to focus primarily on coarse-filter approaches, with the expectation that currently abundant species will remain abundant, and that sensitive but stable wildlife populations will, by and large, persist. The problem with this approach is that the NFMA includes clear requirements to provide for a diversity of plant and animal species, not just a range of ecological conditions that may or may not support diversity. In the end, habitat is a meaningless concept if it is never occupied by actual individuals of the species in question.

With the new rule, the USFS faces a new set of decisions that it can address from a position of power, with greater discretion over its approach to wildlife, and forest management in general. It has the opportunity to improve upon past efforts to conserve wildlife and biological diversity, or it could retreat from the responsibilities established in the NFMA and the 1982 rule. At this juncture, the USFS and the broader community of foresters and wildlife managers should pause to consider whether a relaxation of standards—most notably with respect to population viability—and the consequent lessening of agency responsibility and authority is in the best interest of the nation or the agency itself. We respectfully argue that conservation of the nation's biological wealth, including the persistence of viable populations of wildlife species, is an important service that a strong and professional USFS can and should provide to the American public. To the extent that the agency uses its new discretion to lessen its responsibility to wildlife and its exposure to controversy and criticism, the 2012 rule is likely to represent a retreat from an essential public responsibility and a blow to the wildlife profession. But to the extent that the agency signals its leadership on these issues by voluntary committing itself to a nationwide, science-based, and outcome-oriented program of adaptive management of both forest ecosystems and their full complement of species, the 2012 rule will signal a new era of leadership, where increased discretion is used to elevate intent and expectations, accept greater responsibility, and provide energetic leadership in the conservation and management of the nation's public lands and wildlife.

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LITERATURE CITED

Barnosky, A. D., E. A. Hadly, J. Bascompte, E. L. Berlow, J. H. Brown, M. Fortelius, W. M. Getz, J. Harte, A. Hastings, P. A. Marquet, N. D. Martinez, A. Mooers, P. Roopnarine, G. Vermeij, J. W. Williams, R. Gillespie, J. Kitzes, C. Marshall, N. Matzke, D. P. Mindell, E. Revilla, and A. B. Smith. 2012. Approaching a state shift in Earth's biosphere. Nature 486:52–58.

Beissinger, S. R., and D. R. McCullough. 2002. Population viability analysis. University of Chicago Press, Chicago, Illinois, USA.

Biber, E. 2009. Too many things to do: how to deal with the dysfunctions of multiple-goal agencies. Harvard Environmental Law Review 33:1–63.

Biber, E. 2011. The problem of environmental monitoring. University of Colorado Law Review 83:1–82.

Blumm, M. C., and S. L. Bosse. 2007. Norton v. SUWA and the unraveling of federal public land planning. Duke Environmental Law and Policy Forum 18:105–160.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology 13:805–814.

Center for Biological Diversity. 2012. Status of Center for Biological Diversity and WildEarth Guardians 834 Species Settlements. Center for Biological Diversity, Tucson, Arizona, USA.

Committee of Scientists. 1999. Sustaining the people's land: recommendations for stewardship of the national forests and grasslands into the next century. USFS, Washington, D.C., USA.

Corbin, G. D. 1999. The United States Forest Service's response to biodiversity science. Environmental Law 29:377–415.

Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4:72–85.

Cushman, S. A., K. S. McKelvey, C. H. Flather, and K. McGarigal. 2008. Do forest community types provide a sufficient basis to evaluate biological diversity? Frontiers in Ecology and the Environment 6:13–17.

Cushman, S. A., K. S. McKelvey, B. R. Noon, and K. McGarigal. 2010. Use of abundance of one species as a surrogate for abundance of others. Conservation Biology 24:830–840.

den Boer, P. J. 1981. On the survival of populations in a heterogeneous and variable environment. Oecologia 50:39–53.

Doremus, H. 2008. Data gaps in natural resource management: sniffing for leaks along the information pipeline. Indiana Law Journal 83:407–461.

Duncan, S. L., and J. R. Thompson. 2006. Forest plans and ad hoc scientist groups in the1990s: coping with the Forest Service viability clause. Forest Policy and Economics 9:32–41.

Flather, C. H., K. R. Wilson, and S. A. Shriner. 2009. Geographic approaches to biodiversity conservation: implication of scale and error to landscape planning. Pages 85–121 *in* J. J. Millspaugh and F. R. Thompson, III, editors. Models for planning wildlife conservation in large landscapes. Academic Press, New York, New York, USA.

Government Accountability Office. 1997. Forest Service decision-making: a framework for improving performance. Government Accountability Office, Washington, D.C., USA.

Greenwald, D. N., K. F. Suckling, and M. Taylor. 2006. The listing record. Pages 51–67 *in* D. Goble, J. M. Scott, and F. W. Davis, editors. The Endangered Species Act at thirty. Volume 1. Island Press, Washington, D.C., USA.

Harris, G., and S. L. Pimm. 2008. Range size and extinction risk in forest birds. Conservation Biology 22:163–171.

Harris, S. 2011. Statement of Harris Sherman, on H.R. 1408, to provide for the settlement of certain claims under the Alaska Native Claims Settlement Act. Legislative hearing before the Committee on Natural Resources. U.S. House of Representatives, Washington, D.C., USA.

Haufler, J. B., C. A. Mehl, and G. J. Roloff. 1996. Using a coarse-filter approach with species assessments for ecosystem management. Wildlife Society Bulletin 24:200–208.

Hooper, D. U., F. S. Chapin, III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108.

Houck, O. A. 1997. On the law of biodiversity and ecosystem management. Minnesota Law Review 81:869–979.

Hunter, M. L., Jr. 1990. Wildlife, forests, and forestry: principles of managing forests for biological diversity. Regents/Prentice Hall, Englewood Cliffs, New Jersey, USA.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

MacKenzie, D. I., and J. D. Nichols. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27:461–467.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, Amsterdam, The Netherlands.

Magurran, A. E., and P. A. Henderson. 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422:714–716.

Manley, P. N., M. D. Schlesinger, J. K. Roth, and B. Van Horne. 2005. A field-based evaluation of a presence-absence protocol for monitoring ecoregional-scale biodiversity. Journal of Wildlife Management 69:950–966.

Manley, P. N., W. J. Zielinski, M. D. Schlesinger, and S. R. Mori. 2004. Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. Ecological Applications 14:296–310.

Mills, L. S., M. E. Soule, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. BioScience 43:219–224.

Naeem S., D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. 2009. Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective. Oxford University Press, New York, New York, USA.

Neel, M. C., A. K. Leidner, A. Haines, D. D. Goble, and J. M. Scott. 2012. By the numbers: how is recovery defined by the US Endangered Species Act? BioScience 62:646–657.

Nichols, J. D., and B. K. Williams. 2006. Monitoring for conservation. Trends in Ecology and Evolution 21:668–673.

Nie, M. A., and C. Miller. 2010. National Forest management and private land development: historical, political, and planning considerations. Society & Natural Resources 23:669–678.

Nie, M. A., and C. A. Schultz. 2012. Decision-making triggers in adaptive management. Conservation Biology 26:1137–1144.

Noon, B. R. 2003. Conceptual issues in monitoring ecological resources. Pages 27–72 *in* D. E. Busch and J. C. Trexler, editors. Monitoring ecosystems: interdisciplinary approaches for evaluating ecoregional initiatives. Island Press, Washington, D.C., USA.

Noon, B. R., L. L. Bailey, T. D. Sisk, and K. S. McKelvey. 2012. Efficient species-level monitoring at the landscape scale. Conservation Biology 26:432–441.

Noon, B. R., K. S. McKelvey, and B. G. Dickson, 2009. Multispecies conservation planning on U.S. federal lands. Pages 51–84 *in* J. J. Millspaugh and F. R. Thompson, III, editors. Models for planning wildlife conservation in large landscapes. Academic Press, New York, New York, USA.

Noon B. R., D. D. Murphy, S. R. Beissinger, M. L. Shaffer, and D. DellaSala. 2003. Conservation planning for U.S. national forests: conducting comprehensive biodiversity assessments. BioScience 53:1217–1220.

Noon, B. R., P. Parenteau, and S. C. Trombulak. 2005. Conservation science, biodiversity, and the 2005 U.S. Forest Service regulations. Conservation Biology 19:1359–1361.

Regan, H. M., L. A. Hierl, J. Franklin, D. H. Deutschman, H. L. Schmalbach, C. S. Winchell, and B. S. Johnson. 2008. Species prioritization for monitoring and management in regional multiple species conservation plans. Diversity and Distributions 14:462–471.

Ruggiero, L. F., G. D. Hayward, and J. R. Squires. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. Conservation Biology 8:364–372.

Rylander, J. C. 2012. Recovering endangered species in difficult times: can the ESA go beyond mere salvage? Environmental Law Reporter 42:10017–10023.

Schlossberg, S., and D. I. King. 2009. Modeling animal habitats based on cover types: a critical review. Environmental Management 43:609–618.

Schultz, C. 2010. Challenges in connecting cumulative effects analysis to effective wildlife conservation planning. BioScience 60:545–551.

Schultz, C. A. 2012. The U.S. Forest Service's analysis of cumulative effects to wildlife: a study of legal standards, current practice, and ongoing challenges on a National Forest. Environmental Impact Assessment Review 32:74–81.

Schwartz, M. K., G. Luikart, and R. S. Waples. 2006. Genetic monitoring as a promising tool for conservation and management. Trends in Ecology and Evolution 22:25–33.

Schwartz, M. W. 1999. Choosing the appropriate scale of reserves for conservation. Annual Reviews Ecology and Systematics 30:83–108.

Scott, M. J., D. D. Goble, A. M. Haines, J. A. Wiens, and M. C. Neel. 2010. Conservation-reliant species and the future of conservation. Conservation Letters 3:91–97.

Scott, J. M., D. D. Goble, J. A. Wiens, D. S. Wilcove, M. Bean, and T. Male. 2005. Recovery of imperiled species under the Endangered Species Act: the need for a new approach. Frontiers in Ecology and the Environment 3:383–389.

Soule, M. E., J. A. Estes, B. Miller, and D. L. Honnold. 2005. Strongly interacting species: conservation policy, management, and ethics. BioScience 55:168–176.

Suter, G. W., II. 1993. Ecological risk assessment. Lewis Publishers, Boca Raton, Florida, USA.

U.S. Fish and Wildlife Service [USFWS]. 2007. Queen Charlotte goshawk status review. USFWS, Juneau, Alaska, USA.

U.S. Forest Service [USFS]. 1994. Memorandum of understanding for the conservation of the Robbins' cinquefoil. USFS and USFWS, Washington, D.C., USA.

U.S. Forest Service [USFS]. 1995. Inland native fish strategy: environmental assessment. USFS, Washington, D.C., USA.

U.S. Forest Service [USFS]. 2007. Northern rockies lynx amendment record of decision. USFS, Washington, D.C., USA.

U.S. Forest Service [USFS]. 2011. Biological assessment of the U.S. Department of Agriculture National Forest System land management planning rule for federally listed endangered and threatened species, species proposed for federal listing, species that are candidates for federal listing on National Forest System lands. USFS, Washington, D.C., USA.

U.S. Forest Service [USFS]. 2012. Final programmatic environmental impact statement: National Forest System land management planning. USFS, Washington, D.C., USA.

U.S. Forest Service [USFS] and Bureau of Land Management. 1994. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl; Standards and guidelines for management of habitat for late-successional and old growth forest related species within the range of the northern spotted owl. USFS and Bureau of Land Management, Portland, Oregon, USA.

Van Horne, B. 2002. Approaches to habitat modeling: the tensions between pattern and process and between specificity and generality. Pages 63–72 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C., USA.

Vojta, C. D. 2005. Old dog, new tricks: innovations with presence-absence information. Journal of Wildlife Management 69:845–848.

Waits, L. P. 2004. Using noninvasive genetic sampling to detect and estimate abundance of rare wildlife species. Pages 211–228 *in* W. L. Thompson, editor. Sampling rare and elusive species: concepts, designs, and techniques for estimating population parameters. Island Press, Washington, D.C., USA.

Wilcove, D. S., M. McMillan, and K. C. Winston. 1993. What exactly is an endangered species? An analysis of the U.S. endangered species list: 1985–1991. Conservation Biology 7:87–93.

Wilkinson, C. F. 1992. Crossing the next meridian. Island Press, Washington, D.C., USA.

Wilkinson, C. F., and H. M. Anderson. 1987. Land and resource planning in the national forests. Island Press, Washington, D.C., USA.

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SELECT FEDERAL NATURAL RESOURCE MANAGEMENT COMMITTEE

December 3, 2018

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United States Fish and Wildlife Service
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Re: Black-footed Ferret/Reintroduction in the Thunder Basin National Grassland

Dear Director Talbott, Supervisor Walsh, and Forester Ferebee:

The Select Federal Natural Resource Management Committee of the Wyoming Legislature respectfully requests that your agencies do not include in any future memoranda of understanding or interagency agreements the Thunder Basin National Grassland as a potential location for the reintroduction of black-footed ferrets.

The Committee has carefully considered the issue of black-footed ferrets and prairie dogs on the Grassland throughout the 2018 Interim. At the Committee's meeting in May, the Committee heard from landowners and county commissioners expressing concern about the increase in prairie-dog population, the degradation of habitat in the Grassland due to prairie dogs, and the challenges they have encountered in communicating and working with federal agencies. The county commissioners also discussed expending considerable and scarce funds to implement both lethal and non-lethal strategies to effectively manage the prairie-dog population.

At the Committee's September meeting, the Committee heard from representatives from the Wyoming Game and Fish Department and the United States Fish and Wildlife Service regarding efforts for reintroducing black-footed ferrets and the development of a draft ferret management plan. The plan would call for reintroducing a population of black-footed ferrets in a prairie-dog habitat, but the locations of reintroduction have not yet been determined.

We strongly urge your agencies to not include the Grassland as a potential reintroduction site for black-footed ferrets in any future memorandum of understanding or interagency agreement. There are several issues that must be resolved before reintroduction, including boundary control, dedicated funding for boundary and plague control, and the lack of support from landowners adjacent to the Grassland and in surrounding areas. We also believe that it would be prudent to delay considering the Grassland as a reintroduction site until the Thunder Basin National Grassland Land and Resource Management Plan is amended to allow for better management of the prairie-dog population. In materials provided to the Committee in September, the Wyoming Game and Fish Department, the Wyoming Department of Agriculture, the United States Forest Service, and the United States Fish and Wildlife Service stated that they do not support ferret reintroduction on the Grassland until these issues are resolved.

We note that we support the efforts of any local landowners who wish to be part of reintroduction efforts if they so choose. But currently for the Grassland, we believe it is appropriate to omit it as a potential reintroduction site for any upcoming memorandum of understanding or interagency agreement.

We appreciate your efforts and we hope that the issues surrounding ferret reintroduction on the Grassland are addressed before it is considered as an appropriate site for reintroduction. This is an issue important to legislators, landowners, and community members adjacent to the Grassland. We look forward to continued collaboration with you, your agencies, and agency representatives in the future as we work together to resolve this important issue.

Sincerely,

Senator Michael Von Flatern
Co-Chairman

Representative Tyler Lindholm
Co-Chairman

Cc: John Kennedy, Wyoming Game and Fish Department
Doug Brimeyer, Wyoming Game and Fish Department
Tyler Abbott, United States Fish and Wildlife Service
Russ Bacon, United States Forest Service
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PLOS ONE

RESEARCH ARTICLE

Black-Tailed Prairie Dogs, Cattle, and the Conservation of North America's Arid Grasslands

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Abstract

Prairie dogs (*Cynomys* spp.) have been eliminated from over 95% of their historic range in large part from direct eradication campaigns to reduce their purported competition with cattle for forage. Despite the longstanding importance of this issue to grassland management and conservation, the ecological interactions between cattle and prairie dogs have not been well examined. We address this issue through two complementary experiments to determine if cattle and prairie dogs form a mutualistic grazing association similar to that between prairie dogs and American bison. Our experimental results show that cattle preferentially graze along prairie dog colony edges and use their colony centers for resting, resembling the mutualistic relationship prairie dogs have with American bison. Our results also show that prairie dog colonies are not only an important component of the grassland mosaic for maintaining biodiversity, but also provide benefits to cattle, thereby challenging the longstanding view of prairie dogs as an undesirable pest species in grasslands.

Introduction

Grasslands cover approximately 55 million km^2 (43%) of the terrestrial Earth surface, providing livelihoods for nearly 800 million people, being the most important ecosystem for the provision of the global food supply, and are considered biodiversity hotspots [1]. Yet, grasslands have been subject to intense human pressure due to increasing demand for the expansion of agricultural lands, urbanization, water extraction, and mineral exploitation, causing declines in grassland ecological health and economic productivity [2,3]. Climate change is also important, causing increases in the duration and frequency of droughts, and exacerbating widespread invasion of shrubs into grasslands [4]. In North America, grasslands have dramatically declined; tallgrass, mixed-grass, and shortgrass prairie cover only 1%, 20%, and 30%, of their historical extent, respectively, with the remaining portions being highly fragmented [5,6].

Grasslands are fundamentally shaped by two key functional groups that have co-evolved for thousands of years, namely, large migratory mammalian herbivores and small to medium-sized burrowing herbivorous mammals [7,8]. Both functional groups of herbivores play key-stone and/or ecosystem engineering roles and have complementary and interactive effects on grassland ecosystem structure and function [9–12].

In North America, American bison (*Bison bison*), through their grazing and wallowing, create grazing lawns and increase grassland biodiversity, prevent encroachment of shrubs through trampling and consumption of woody vegetation, and increase nutrient availability through the deposition of dung and urine [13]. Grazing by bison impacts plant survival, stimulates plant nitrogen uptake and aboveground production, and alters grassland community structure and ecosystem processes [14,15].

Prairie dogs also increase habitat heterogeneity and biodiversity of grassland ecosystems by creating islands of unique habitat [12]. Like many other burrowing mammals, prairie dogs are highly social, and aggregate into large colonies where they transform the landscape through their burrowing and foraging activities [16,17]. They are prey of a wide variety to predators and their borrows provide refuge for numerous animals [18]. Prairie dog grazing increases forage quality by reducing leaf age and enhancing plant nitrogen uptake, attracting large herbivores to their colonies [19,20]. The center of the prairie dog colonies, where most borrow-mounds appear, is dominated by bare ground and a low mat of heavily-grazed forbs and a mix of perennial and annual grasses [21]. In contrast, the edges of the colonies, which experience less impact by prairie dogs, are characterized by fewer burrows, taller vegetation, and moderately grazed annual and perennial grasses [21]. Prairie dogs also maintain the presence of grasslands and prevent their succession into shrubland by clipping shrubs and consuming their seedlings [12,22].

Bison and prairie dogs have co-evolved for thousands of years and constitute a grazing association, whereby bison preferentially graze along the edges of prairie dog colonies because of the availability of high quality forage; they also tend to rest within the center of colonies [19,23]. Bison that graze within prairie dog colonies have been shown to gain more weight compared to those that feed in off-colony grasslands [24]. Likewise, bison benefit prairie dogs by increasing nutrient quality of vegetation through their grazing and deposition of dung and urine [19,23,25], and their grazing lowers vegetation height, improving the ability of prairie dogs to detect predators [26].

Black-tailed prairie dogs (*Cynomys ludovicianus*) historically ranged across 40 million hectares of North America's central grasslands. But, their populations have declined by more than 98% primarily as a result of habitat loss to agriculture, introduction of plague from Eurasia, and eradication campaigns designed to eliminate their purported competition with cattle for grazing resources [8,27,28]. In addition to the expenditure of millions of public tax dollars on eradication efforts to support private industry, the loss of prairie dogs has had a dramatic consequences on the ecological integrity of North America's grassland ecosystem. The decline in prairie dogs is largely responsible for the near extinction of the black-footed ferret (*Mustela nigripens*), declines in other prairie dog-dependent species, encroachment of mesquite (*Prosopis glandulosa*) and other woody shrubs dispersed by cattle, and reduction in the economic productivity of this ecosystem [27–30]. Despite research showing that management strategies utilizing large-scale, lethal-control are neither scientifically justified nor cost effective, these "control" programs are still employed today and remain funded by taxpayers [7,12,31,32].

Domestic cattle (*Bos taurus*) have largely supplanted native American bison which were near-exterminated during the 19th century [13,33]. Bison and cattle are ecologically similar, [13] and while overgrazing by cattle has caused widespread desertification because of poor rangeland management [28,34], the activities of domestic cattle may partially substitute the functional role of the American bison [13,35,36]. In fact, cattle and prairie dogs seem to have a grazing association similar to that of bison and prairie dogs, with important interactive impacts on grasslands [8,27,37,38]. Cattle are frequent visitors to black-tailed prairie dog colonies [39,40], and in some areas where conservative grazing management schemes are employed, prairie dog populations have increased up to two-fold [8].

The Janos Biosphere Reserve (JBR), located in northwest Chihuahua, Mexico maintains one of the largest remnants of desert grassland in northwestern Mexico, and one of the largest remaining prairie dog colony complexes in North America [28,41]. Like most of the semi-arid grassland ecosystems in North America, the Janos grasslands have been transformed by the synergistic effects of chronic overgrazing due to poor cattle management, drought and climate change, and the expansion of industrial agriculture [28,41]. These changes in the Janos region have resulted in a 75% decline of the once 55,000 ha prairie dog complex, and widspread expansion of shrublands into native grasslands [28,41].

Despite the longstanding importance of effective and conservation-based management of grasslands, the ecological interactions between cattle and prairie dogs remains little studied [12]. Understanding and applying the ecological principles of the interactions between cattle and prairie dog is fundamental to informing sustainable grassland management policies and procedures. To understand this interaction and the impact on grassland health, we studied the ecological relationships between cattle and prairie dogs in the desert grasslands of the Janos Biosphere Reserve, Chihuahua, Mexico.

Our objective was to determine if cattle and prairie dogs form grazing associations similar to those described between prairie dogs and American bison [23,26]. We specifically addressed the following questions: i) Do cattle have habitat preferences for prairie dog colonies or other habitat types? ii) Do cattle show temporal variability in habitat selection, as bison do? iii) Do cattle selectively graze in particular areas of prairie dog colonies, such as colony edges? and iv) How can the results from this research be applied to conservation strategies for semi-arid grasslands?

Materials and Methods

Study site

We conducted our research within a 1,700 ha fenced area (30° 52’ 58.13” N, 108° 27’ 21.64” W) located in the “El Uno” Ecological Reserve within the Janos Biosphere Reserve, Chihuahua, northwestern Mexico [41]. Native annual grasses dominate the plant community, while native perennial grasses are sparse [8]. The mean annual precipitation in the region is 317 mm, and most of it occurs during the summer monsoon period. The mean annual temperature is 16.95°C [42].

Experimental design

We conducted two complementary experiments to understand the relationship between habitat selection by cattle and the presence of black-tailed prairie dog colonies: 1) a Large-scale cattle habitat preference experiment and 2) a Small-scale cattle grazing preference experiment (descriptions provided below). We repeated all the design elements of each experiment three times from 2006–2007 in order to capture cattle grazing behavior under different periods of plant productivity: 1) low forage availability during the summer dry season (June-July) in 2006; 2) high forage availability at the end of the growing season in the fall (September-October) in 2006; and 3) the grass dormancy season during the winter (December-January) in 2006/2007. Both experiments were conducted using the recommended conservative grazing conditions

(<40% use of available forage) [43], with the suggested stocking rate for this region being roughly 30–60 hectare by animal unit considering a 50% available forage consumption [44,45], because our goal, here, was to understand the ecological relationships between domestic cattle and black-tailed prairie dogs under conservative grazing.

Transportation and handling of domestic cattle in both experiments was according to the Norma Oficial Mexicana / Oficial Mexican Norm NOM-051-ZOO-1995 (Trato humanitario en la movilizacion de animales / Humanitarian treatment in animal mobilization) [46]. We followed low stress handling techniques performed by trained cattle technicians, in order to avoid stress and ensure humane treatment of all animals used in our study. No official permit was necessary to perform this experiment because pasture raised domestic cattle are not considered an experimental animal species under the Norma Oficial Mexicana NOM-062-ZOO-1999 (Especificaciones tecnicas para la produccion, cuidado y uso de los animales de laboratorio / Technical specifications for production, care and use of lab animals) [47]. All the facilities used in both experiments (trailer, paddocks, GPS collars and electric fences) were commercial equipment designed for cattle management. For the use of GPS collars we followed the American Society of Mastozoology recommendations [48]. Additionally, the animals were routinely observed and checked by a trained veterinarian. All the permissions and permits required for fieldwork and utilization of domestic cattle were requested and authorized by the cattle owners and the administration of The Nature Conservancy's "El Uno" Ecological Reserve.

Large-scale cattle habitat preference experiment

The first experiment assessed cattle habitat preference (vegetation types) by activity type (grazing, resting and walking) within a 1,700 ha pasture. We followed the movements of 36 cows (*Bos taurus*), randomly separated into three replicated groups of 12 individuals, to evaluate cattle habitat selection. Each cow was fitted with a Global Position System (GPS) collar equipped with movement sensors (Lotek, 2200LR) programmed to record spatial locations every 5-minutes. Cows were allowed to graze freely and move throughout the pasture for 6 consecutive days. Only the 12 cows fitted with the GPS collars where present within 1,700 ha pasture at the time, which represents 141 ha by animal unit. To record cattle activities, we used movement sensor data together and cattle movement patterns (see Peinetti *et al*. 2011 for details in the Peinetti s) [49].

We used a QuickBird satellite image with 0.6 m resolution object-oriented classification (see Laliberte *et al*. 2007) [50] to develop a vegetation map, enabling us to assess habitats with which cattle most associated. We identified six vegetation types: 1) Annual grassland [which covered 50% of the pasture and was dominated by six weeks three awn (*Aristida adscencionis*)]; 2) perennial gramma grassland [14% cover, dominated by perennial blue grama (*Bouteloua gracilis*.)]; 3) tobosa grassland [10% cover, dominated by tobosa, *Hilaria mutica*]; 4) vine mesquite grassland [8% cover, dominated by vine mesquite, *Panicum obtusum*]; 5) weedy annual forbs [5% cover; dominated by Russian thistle, *Salsola kali* & Palmer's amaranth *(Amaranthus palmeri*]; and 6) prairie dog colonies [12% cover] (Fig. 1).

Data analysis. We performed a multivariate analysis of variance (MANOVA) with Repeated Measurements Analysis of Variance, to test the hypothesis of no difference in cattle habitat selection (location x vegetation) by activity and season, to test the null hypothesis of there being no variation in cattle habitat selection (records x vegetation) by activity and season. When the MANOVA tests where significant, we used general linear models (GLM) to identify the source of variation. There were no significant differences among replicates (i.e., 12 cow group) within seasons, so we performed complementary Chi-Square Goodness-of-Fit Test by season (all season locations x vegetation) to test the null hypothesis of random habitat use by

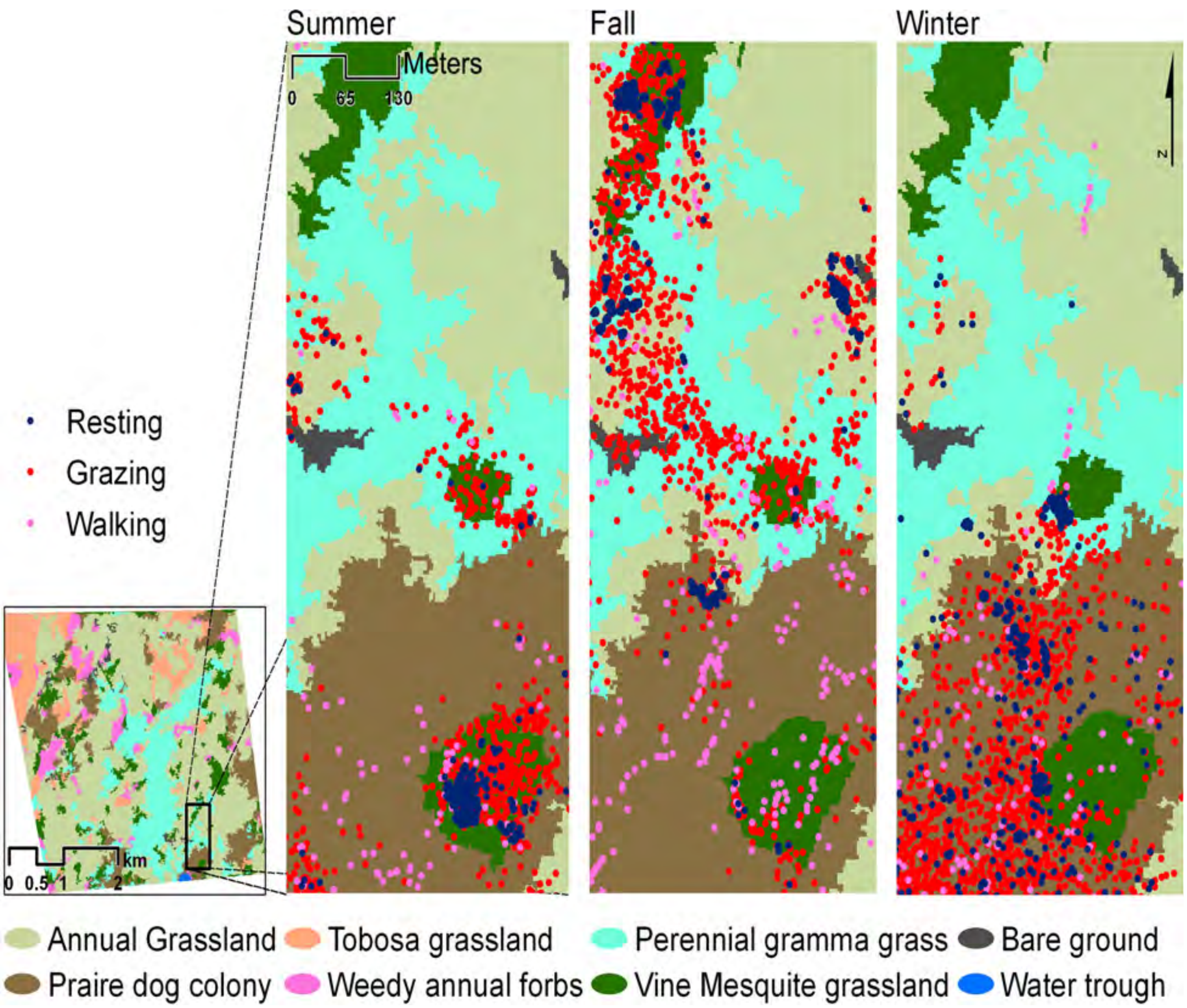

Fig 1. Spatial pattern of the three classes of cattle activity relative to the vegetation/ground cover types through seasons. Colored dots indicate cattle locations by activity across all weeks during each sample season.

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activity (activity x vegetation). To determine the type of vegetation cattle preferred by activity by season, within the pasture, we used Bonferroni confidence intervals, calculating the percent cattle used each habitat type. When the percentage of availability of any given vegetation type was below the confidence interval, we considered it to have been significantly selected ($P < 0.001$). When availability was above the confidence interval, that particular habitat was significantly avoided.

Small-scale cattle grazing preference experiment

We conducted a second experiment to determine if cattle preferentially forage on a particular section of prairie dog colonies (i.e., grazing zones): the colony center, along colony edges, or off colonies. To identify the grazing patterns, we established in three independent prairie dog colonies, three blocks containing three 60 m X 60 m experimental plots. A cattle-grade electric fence enclosed each plot and encompassed the three grazing zones. To determine if cattle grazing location preference changes with the proportion of colony occupancy of the landscape, we varied the proportion of the grazing zones across the three plots on each colony: plot 1 consisted of 25% prairie dog colony and 75% off-colony grassland; plot 2 consisted of 50% prairie dog colony and 50% off-colony grassland; and plot 3 consisted of 75% prairie dog colony and 25% off-colony grassland. We calculated the prairie dog colony edge area for each plot by multiplying the average edge width by its length, using ArcMap 9.0 (ESRI). Four cows grazed each plot for 4 hours with a stocking rate of 65 ha by animal unit, once each season during the early morning grazing activity peak [51]. We recorded the type of cattle activity (grazing, resting and walking) observed for each cow within each plot every three minutes from a portable observation tower located 30 m from the edge of each plot.

Data analysis We performed a multivariate analysis of variance (MANOVA) with a Repeated Measurements Analysis approach to test the null hypothesis of cattle grazing zone selection by season. When MANOVA tests where significant, we performed a Chi-Square-Goodness-of-Fit to make comparisons of the cattle grazing zones (grazing x zone) by season. We also used Bonferroni confidence intervals to determine the preferred grazing zone; only grazing records where used in this analysis.

All data were assessed for normality, and if needed, normalized by log transformations using JMP version 8.

Results

Large-scale cattle habitat preference experiment

Cattle showed strong use preferences for prairie dog colonies, perennial gramma grassland, vine mesquite grassland and grassland dominated by annual weedy forbs (i.e., habitats used above their availability). In contrast, annual grassland and tobosa grassland were avoided (i.e., utilization below availability) (Fig. 1). Despite prairie dogs occupying only 12% of the landscape, cattle associated with colonies more than 24% of the total time; whereas, while annual grasslands covered 50% of the total area, cattle utilized them less than 20% of the time (Fig. 2 and Table 1).

Cattle habitat selection also differed seasonally (MANOVA: $P < 0.0001$; $F_{2.8} = 7.8e\text{-}5$). Activity locations varied across the three seasons (MANOVA $P < 0.035$; $F_{1.6} = 0.007$) and activities (i.e., grazing, resting, walking) (MANOVA: $P < 0.001$; $F_{4.27} = 0.03$ (Fig. 1). The chi-square values for cattle activity by season were: Grazing, summer $X^2 = 16{,}406.4$, $P = 0.05$; fall $X^2 = 8119.1$, $P = 0.05$; winter $X^2 = 8{,}282.67$, $P = 0.05$; Resting, summer $X^2 = 132{,}806$; $P = 0.05$, fall $X^2 = 36{,}234.4$, $P = 0.05$; winter $X^2 = 15{,}014.60$, $P = 0.05$; Walking, summer $X^2 = 32{,}806.1$, $P = 0.05$; fall $X^2 = 978.7$, $P = 0.05$; winter $X^2 = 1{,}724.6$, $P = 0.05$ (Fig. 2 and Table 1). Seasonal changes in location x vegetation by activity, were detected only for prairie dog colonies (GLM: $P = 0.02$, $F = 4.86$; P 0.02, $F = 8.40$, respectively) and vine mesquite grassland (GLM: $P = 0.05$, $F = 3.44$; $P < 0.0001$, $F = 22.4$, respectively). Use of annual weedy forbs differed by activity but not by season (GLM: $P = 0.001$, $F = 10.32$).

Small-scale cattle grazing preference experiment

Cattle used prairie dog colonies for grazing and resting at rates above their availability during both the high forage availability season, in fall, and the grass dormancy season, in winter ($P < 0.001$), (Fig. 2 and Table 1).

There were no significant differences among the three plots across the three blocks (MANOVA $F_{1.2} = 0.79$, $P < 0.2$), meaning no variation between treatments and prairie dog colonies, but strong seasonal preferences for particular foraging zones were detected (MANOVA $F_{4.5} = 0.2035$, $P < 0.0001$). The chi-square values for cattle grazing locations by foraging zone were:

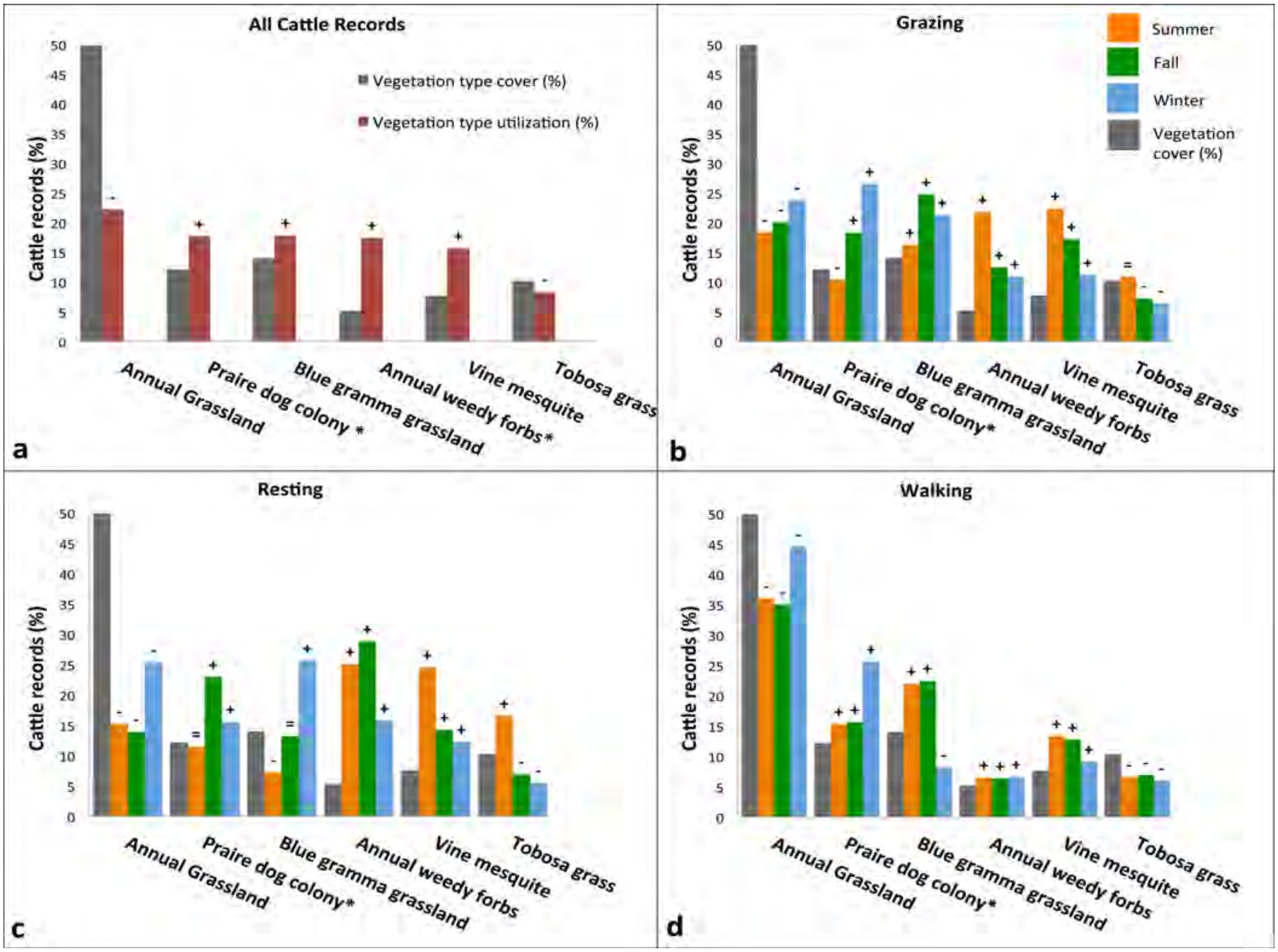

Fig 2. Large-scale experiment. Cattle record's percentage by vegetation type, activity, and season. a) Total time cattle utilized the different vegetation types v.s. vegetation type % cover; b) Grazzing records by vegetation by season v.s. vegetation type cover %; c) Grazzing records by vegetation x season v.s. vegetation type cover %. d) Grazzing records by vegetation x season v.s. vegetation type cover %. Bonferroni confidence-interval results (P <0.001) are given by the following signs: "**+**" indicates preference (utilization above availability); "**=**" indicates random (utilization equal to its availability); and "–" indicates avoidance (utilization below its availability); and "*****" indicates vegetation types with significant differences in utilization across seasons.

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$X^2 = 619.2$, summer; $X^2 = 851.51$, fall; $X^2 = 2,813.6$, winter, denoting a strong non-random utilization pattern.

Prairie dog colony edges were preferentially selected for grazing by cattle across all seasons and were the most utilized foraging zone during the winter season ($P < 0.001$, Fig. 3, Table 2). More than 50% of the grazing events occurred in only 7% of the total experimental area, being represented by the colony edges. Unlike the colony edge, cattle consistently avoided grazing within the prairie dog colony center across all seasons ($P < 0.001$) (Fig. 3, Table 2).

Discussion

We found that cattle preferred foraging on prairie dog colonies in Chihuahuan desert grasslands, especially during the winter grass dormancy season but also during the fall. Results from this large-scale habitat selection experiment also were consistent with our small-scale grazing preference experiment on cattle foraging behavior in relationship to prairie dog colonies.

Table 1. Large-scale experiment.

	Large-scale cattle habitat preference experiment Bonferroni confidence-interval analysis					
Vegetation Type	**Expected proportion**	**Confidence interval of occurrence $(P > 0.001)$**	**Season**	**Activity**	**Proportion observed**	**Utilization**
Annual grassland	0.49	$0.488 < P < 0.507$	Summer	Grazing	0.18	-
				Resting	0.15	-
				Walking	0.35	-
			Fall	Grazing	0.19	-
				Resting	0.13	-
				Walking	0.34	-
			Winter	Grazing	0.23	-
				Resting	0.24	-
				Walking	0.44	-
Perennial gramma grassland	0.14	$0.133 < P < 0.146$	Summer	Grazing	0.16	+
				Resting	0.07	-
				Walking	0.21	+
			Fall	Grazing	0.24	+
				Resting	0.131	-
				Walking	0.22	+
			Winter	Grazing	0.21	+
				Resting	0.25	+
				Walking	0.08	-
Prairie dog colony	0.12	$0.114 < P < 0.127$	Summer	Grazing	0.10	-
				Resting	0.114	=
				Walking	0.15	+
			Fall	Grazing	0.18	+
				Resting	0.22	+
				Walking	0.15	+
			Winter	Grazing	0.26	+
				Resting	0.15	+
				Walking	0.25	+
Tobosa grassland	0.10	$0.096 < P < 0.108$	Summer	Grazing	0.108	=
				Resting	0.16	+
				Walking	0.06	-
			Fall	Grazing	0.07	-
				Resting	0.06	-
				Walking	0.06	-
			Winter	Grazing	0.06	-
				Resting	0.05	-
				Walking	0.05	-

(*Continued*)

Table 1. (*Continued*)

Large-scale cattle habitat preference experiment Bonferroni confidence-interval analysis						
Vegetation Type	**Expected proportion**	**Confidence interval of occurrence (P> 0.001)**	**Season**	**Activity**	**Proportion observed**	**Utilization**
Vine mesquite grassland	0.07	0.071 <P< 0.081	Summer	Grazing	0.22	+
				Resting	0.24	+
				Walking	0.13	+
			Fall	Grazing	0.16	+
				Resting	0.14	+
				Walking	0.12	+
			Winter	Grazing	0.11	+
				Resting	0.12	+
				Walking	0.90	+
Weedy annual forbs	0.05	0.047 <P< 0.056	Summer	Grazing	0.21	+
				Resting	0.25	+
				Walking	0.06	+
			Fall	Grazing	0.12	+
				Resting	0.28	
				Walking	0.06	+
			Winter	Grazing	0.10	+
				Resting	0.15	+
				Walking	0.66	+
Bare ground	0.008	0.007 <P< 0.010	Summer	Grazing	0.001	-
				Resting	0.0	-
				Walking	0.0	-
			Fall	Grazing	0.015	-
				Resting	0.009	=
				Walking	0.01	+
			Winter	Grazing	0.006	-
				Resting	0.01	+
				Walking	0.0	-

Cattle record's percentage by vegetation type, activity, and season. Bonferroni confidence-interval results (P <0.001) are given by the following signs: "+" indicates preference (utilization above availability); "=" indicates random (utilization equal to its availability); and "–" indicates avoidance (utilization below its availability).

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During winter and fall seasons when cattle preferred prairie dog colonies for grazing, cattle spent most of their time grazing along the edges of colonies where forage quality is often higher than in off colony areas and where quantity is higher compared to colony centers [19,23,25]. In summer, when cattle did not prefer prairie dog colonies for grazing, cattle spent most of their foraging time off colonies, within the surrounding grassland, resembling the previously described American bison-prairie dog grazing association [7,12,18,19,23,25,27].

In our study, cattle grazed and rested on prairie dog colonies in the fall during the grass-growing season and especially in the winter during the grass dormancy season, suggesting that prairie dog colonies provide an important forage resource within the greater grassland landscape and during one of the harshest seasons for cattle grazing. These patterns probably resulted from prairie dog activities during the grass growing season that enhance forage quality, such as removal of standing dead biomass and clipping of vegetation that increases plant

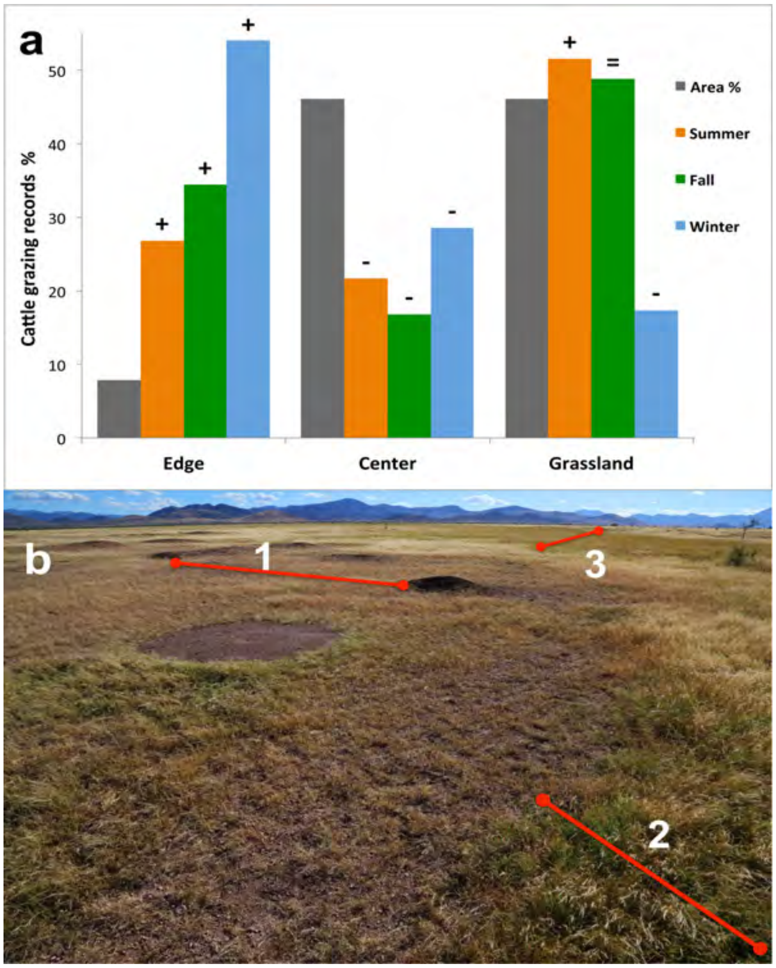

Fig 3. Small-scale experiment. Cattle grazing record's percentage by foraging zone and season v.s. foraging zone area cover %. (a) Bonferroni confidence-interval results (P <0.001) are given by the following signs: "**+**" indicates preference (utilization above availability); "**=**" indicates random (utilization equal to its availability); and "–" indicates avoidance (utilization below its availability); (b) image of a typical prairie dog colony in the Janos grasslands, showing vegetation height and cover increasing away from the colony center (1) towards the colony edge (2) and the surrounding climax grasslands (3).

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nitrogen uptake, in addition to the lack of other more palatable forage options during the winter season [20,52].

Foraging behavior is strongly influenced by dietary preferences, and large herbivores spend more time grazing in plant communities that have higher quantities of preferred forage [53]. While cattle showed strong preferences for foraging on prairie dog colonies in our study, they also associated with other vegetation types. They spent considerable time in perennial gramma grassland, vine mesquite grassland and annual weedy forb habitat, but avoided tobosa grassland and annual grassland, the latter being the most abundant vegetation type within the Janos region. In North American grasslands, cattle prefer perennial grasses like blue gramma (*Bouteluoa gracilis*) and vine mesquite (*Panicum obtusum*), which have their highest nutritional value during the summer and fall [49,54,55]. Annual grasses, such as the six weeks three awn have comparatively limited nutritional value; and other, more desert-adapted perennial grasses, such as tobosa grass, contains an abundant accumulated dead plant material which make them unpalatable [56].

Table 2. Small-scale experiment.

Small-scale cattle grazing preference experiment Bonferroni confidence-interval analysis

Season	Foraging Zone	Expected Proportion	Proportion observed	Confidence interval of occurrence ($P > 0.001$)	Use
Summer $x^2 = 619.2$ $P < 0.005$	Margin	0.071	0.268	$0.048 < P < 0.094$	+
	Center	0.463	0.216	$0.419 < P < 0.509$	-
	Grassland	0.463	0.515	$0.419 < P < 0.509$	+
Fall $x^2 = 851.51$ $P < 0.005$	Margin	0.068	0.343	$0.041 < P < 0.095$	+
	Center	0.464	0.168	$0.415 < P < 0.518$	-
	Grassland	0.465	0.487	$0.415 < P < 0.518$	+
Winter $x^2 = 2813.6$ $P < 0.005$	Margin	0.095	0.540	$0.072 < P < 0.228$	+
	Center	0.452	0.285	$0.413 < P < 0.490$	-
	Grassland	0.452	0.173	$0.413 < P < 0.490$	-

Cattle grazing record's percentage by foraging zone and season v.s. foraging zone area cover %. Bonferroni confidence-interval results ($P < 0.001$) are given by the following signs: "+" indicates preference (utilization above availability); "=" indicates random (utilization equal to its availability); and "–" indicates avoidance (utilization below its availability).

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Cattle foraging behavior varies seasonally with plant phenological and nutritional changes [10]. Perennial grasses and weedy annual forbs begin to green-up at the end of the spring into the beginning of summer, and are at this time, preferred forage by cattle. Growth of perennial grasses accelerates following the summer rains through fall, developing new foliage and pushing off dead remnants from the preceding dormancy season, increasing their palatability [57]; whereas in summer weedy forbs flower, form sharp spines and accumulate anti-herbivore compounds, so cattle avoid them [58]. During winter, nutritional quality of perennial grasses declines, reducing their consumption by cattle, and consumption of seasonal forbs increases [59]. Our findings, consequently, demonstrate the importance of heterogeneity within semi-arid grasslands, which includes prairie dog colonies, for the provision of multiple forage alternatives temporally and spatially within semi-arid grassland landscapes [34,60]. The preferential foraging on prairie dog colonies by cattle highlights not only the role of prairie dogs in creating heterogeneous grassland landscapes, [8,27] but also their important contribution to supporting local communities that depend on cattle grazing for their livelihoods.

Our results not only support previous studies showing that cattle occur more commonly on prairie dog colonies in the Chihuahuan Desert grasslands [40], but also that cattle preferentially forage on them. However, these ecological relationships between cattle and prairie dogs probably vary across the geographic ranges and different species of prairie dogs, and with variation in precipitation and plant productivity [52]. For example, in the mixed-grass prairie, cattle spend significantly more time in pastures with prairie dog colonies compared to pastures without colonies [39]. In contrast, cattle do not appear to associate with prairie dog colonies in shortgrass prairies [38]. When comparing the weights of cattle that graze in areas with prairie dog colonies (at < 30% pasture occupancy) and areas without prairie dog colonies, no significant difference in cattle weight gains have been found, presumably because the reduction of available forage on colonies is compensated for by the improved vegetation quality [44,45]. Nevertheless, weight gains can decline in shortgrass prairie when colonies occupy more than 30% of the total area, and when prairie dog colonies occupy more than 60% of the total area, cattle weight gain is reduced further (14%) [61,62].

Our work suggest that prairie dogs and cattle can have a positive, mutualistic relationship, in North America's desert grasslands [8,37]. Cattle appear to benefit from modified vegetation structure and composition and increased nutritional value on prairie dog colonies [12,52,61]. Similarly, prairie dogs are known to benefit from the presence of large grazers, like bison and cattle [12,19,23,25,27,37]. For example, black-tailed prairie dog density increased about 2-fold under conservative cattle grazing, on a companion study located adjacent to ours [8]. Cattle grazing positively affected prairie dog abundances, likely by improving their ability to see predators [8,12,27,39]. Similar results have been reported for Utah prairie dogs (*C. parvidens*), which prefer foraging in areas grazed moderately by cattle compared to non-grazed areas [63]. Additionally, others have observed that prairie dogs establish their colonies in areas that are intensively grazed by livestock [39]. Similar to the effects of American bison, cattle stimulate nitrogen uptake and lower leaf age through their grazing, and increase available nitrogen by depositing dung and urine [13,34]. So, like bison, cattle also may positively impact prairie dogs by increasing forage quality [23,38,63,64]. This ecological relationship is similar to the grazing association between prairie dogs and bison [19,23,25].

Management

This positive relationship between cattle and prairie dogs in the Chihuahuan Desert grasslands, challenges the long-standing view of prairie dogs as an undesirable pest species in rangelands [31]. The presence of prairie dogs can have a positive impact on cattle that is beneficial to the livestock industry, by prairie dog colonies providing favorable grazing habitat for cattle and reducing shrub invasion into grassland environments [22,28]. In turn, cattle can be used as a management tool to strategically graze areas where prairie dogs are needed to help promote biodiversity, enhance forage quality, and reduce shrub encroachment [34]. In sum, our work, along with that by Davidson, 2010, suggests that prairie dogs and cattle can have a mutualistic relationship. And, when their abundances are managed so that they interact synergistically together, they can enhance the productivity and biodiversity of grassland ecosystems [8], supporting local communities that depend on livestock grazing for their livelihoods and the livestock industry more generally.

A paradigm shift is needed on how rangelands are managed, from simply promoting maximization of livestock production and creating homogenous grassland landscapes dominated by only a few desirable forage species, to more integral management that benefits biodiversity, enhances habitat heterogeneity, and improves ecosystem services on which humans depend [34,60]. Given the widespread degradation of grasslands and loss to shrublands, the results of our work provide new insights into novel management strategies for grassland conservation and a potential win-win scenario for biodiversity and productive human activities. In addition to the possible direct benefits to cattle ranching and increasing grassland biodiversity, prairie dogs also increase groundwater recharge, forage availability, soil carbon storage, regulation of soil erosion, and regulation of soil productive potential [16]. Despite increasing awareness of the important functional role of prairie dogs, they are still considered a pest by range managers and still commonly subject to lethal control in both the US and Mexico [12]. Our research supports the argument that conservation and restoration of prairie dog populations should be key components of sustainable grassland management, and that conservation-guided cattle ranching can be a productive human enterprise, compatible with grassland biodiversity conservation objectives.

Supporting Information

S1 File. Norma Oficial Mexicana NOM-051-ZOO-1995, Trato humanitario en la movilización de animales.
(PDF)

S2 File. Norma Oficial Mexicana NOM-062-ZOO-1999, Especificaciones técnicas para la producción, cuidado y uso de los animales de laboratorio.
(PDF)

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Author Contributions

Conceived and designed the experiments: RSC ELF GC. Performed the experiments: RSC ELF EPG. Analyzed the data: RSC HLS HSA. Contributed reagents/materials/analysis tools: RSC AD HLS. Wrote the paper: RSC AD GC HLS HSA EPG.

References

1. Gilles L, Jhon H, Abad C. Introduction: Food Security and Environmental Impacts- Challenge for Grassland Sciences. In: Gilles L, Jhon H, Abad C, editors. Grassland Productivity and Ecosystem Services. Wallingford, Oxfordshire; Cambridge, M.A.: CABI; 2011. p. xiii–xvii.
2. Fargione JE, Cooper TR, Flaspohler DJ, Hill J, Lehman C, Tilman D, et al. Bioenergy and Wildlife: Threats and Opportunities for Grassland Conservation. Bioscience. 2009 Oct; 59(9):767–77.
3. Okin G. Toward a Unified View of Biophysical Land Degradation Processes in Arid and Semi-arid Lands. In: Reynolds JF, Stafford Smith DM, editors. Global Desertification: Do Humans Cause Deserts? Berlin: Dahlem University Press; 2002. p. 95–109.
4. McCarty JP. Ecological Consequences of Recent Climate Change. Conserv Biol. 2001 Apr; 15 (2):320–31.
5. Gauthier DA, Wiken E. The Great Plains of North America. PARKS. 1998; 8(3):9–20.
6. Samson F, Knopf F. Prairie conservation in North America. Bioscience. 1994; 44(6):418–21.
7. Delibes-Mateos M, Smith AT, Slobodchikoff CN, Swenson JE. The paradox of keystone species persecuted as pests: A call for the conservation of abundant small mammals in their native range. Biol Conserv. Elsevier Ltd; 2011 May; 144(5):1335–46.
8. Davidson AD, Ponce E, Lightfoot DC, Fredrickson EL, Brown JH, Cruzado J, et al. Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. Ecology. 2010 Nov; 91(11):3189–200. PMID: 21141180
9. Jones CG, Lawton JH, Shachak M. Organisms as ecosystemen engineers. Oikos. 1994; 69(3):373–86.
10. Augustine DJ, Mcnaughton SJ. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. J Wildl Manage. 1998; 62(4):1165–83.
11. Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills S, et al. Challenges in the Quest for Keystones. Bioscience. 1996; 46(8):609–20.
12. Davidson AD, Detling JK, Brown JH. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. Front Ecol Environ. 2012 Nov; 10(9):477–86.
13. Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, et al. Keystone role of Bison in North American tallgrass prairie. Bioscience. 2010; 49(1):39–50.

14. Frank DA, Mcnaughton SJ, Tracy BF. The ecology of the Earth's grazing ecosystems profound functional exist between the Serengeti similarities and Yellowstone. Bioscience. 1998; 48(7):513–21.
15. Huntly N. Herbivores and the dynamics of communities and ecosystems. Annu Rev Ecol Syst. 1991; 22(1991):477–503.
16. Martinez-Estevez L, Balvanera P, Pacheco J, Ceballos G. Prairie dog declines reduces the supply of ecosystem services and leads to desertification of semiarid grasslands. Proc Natl Acad Sci. 2013;1–26.
17. Miller B, Ceballos G, Reading R. The prairie gog and biotic diversity. Conserv Biol. 1994; 8(3):677–81.
18. Kotliar NB. Application of the keystone-species concept to prairie dogs: How well It work? Conserv Biol. 2000; 14(6):1715–21.
19. Coppock JE, Ellis JE, Detling JK, Dyer MI. Plant-herbivore Interactions in a North American mixed-grass prairie II. Responses of bison to modification of vegetation by prairie dogs. Oecologia. 1983; 56 (1):10–5.
20. Whicker AD, Detling JK. Ecological consequences of prairie dog disturbances. Bioscience. 1988; 38 (11):778–85.
21. Osborn B, Allan PF. Vegetation of an abandoned prairie-dog town in tall grass prairie. Ecology. 1949; 30(3):322–32.
22. Weltzin JF, Archer S, Heitschmidt RK. Small-mammal regulation of vegetation structure in a temperate savanna. Ecology. 1997 Apr; 78(3):751–63.
23. Krueger K. Feeding relationships among bison, pronghorn, and prairie dogs: An experimental analysis. Ecology. 1986; 67(3):760–70.
24. Vanderhye AVR. Interspecific nutritional facilitation: do bison benefit from feeding on prairie dog towns? Colorado State University; 1985. p. 44.
25. Fahnestock JT, Detling JK. Bison-prairie dog-plant interactions in a North American mixed-grass prairie. Oecologia. 2002; 132(1):86–95.
26. Coppock DL, Detling JK. Alteration of bison and black tailed prairie dog grazing interaction by prescribed burning. J Wildl Manage. 1986; 50(3):452–5.
27. Miller BJ, Reading RP, Biggins DE, Detling JK, Forrest SC, Hoogland JL, et al. Prairie dogs: An ecological review and current biopolitics. J Wildl Manage. 2007 Nov; 71(8):2801–10.
28. Ceballos G, Davidson A, List R, Pacheco J, Manzano-Fischer P, Santos-Barrera G, et al. Rapid decline of a grassland system and its ecological and conservation implications. PLoS One. 2010 Jan; 5(1): e8562. doi: 10.1371/journal.pone.0008562 PMID: 20066035
29. Archer S, Garrett MG, Detling JK. Rates of vegetation change associated with prairie dog (Cynomys ludovicianus) grazing in North American mixed-grass prairie. Vegetatio. 1987; 72(3):159–66.
30. Weltzin JF, Dowhower SL, Heitschmidt RK. Prairie dog effects on plant community structure in southern mixed-grass prairie. Southwest Nat. 1997; 42(3):251–8.
31. Jones S. Becoming a pest: Prairie dog ecology and the human economy in the Euroamerican West. Environ Hist Durh N C. 1999; 4:531–52.
32. Bergstrom BJ, Arias LC, Davidson AD, Ferguson AW, Randa L a., Sheffield SR. License to Kill: Reforming Federal Wildlife Control to Restore Biodiversity and Ecosystem Function. Conserv Lett. 2013 Mar 11; 00:1–12.
33. List R, Ceballos G, Curtin C, Gogan PJP, Pacheco J, Truett J. Historic distribution and challenges to bison recovery in the northern Chihuahuan desert. Conserv Biol. 2007 Dec; 21(6):1487–94. doi: 10.1111/j.1523-1739.2007.00810.x PMID: 18173472
34. Derner JD, Lauenroth WK, Stapp P, Augustine DJ. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. Rangel Ecol Manag. 2009; 62(2):111–8. doi: 10.1186/2046-0481-62-2-111 PMID: 21851728
35. Towne EG, Hartnett DC, Cochran RC. Vegetation trends in tallgrass prairie from bison and cattle grazing. Ecol Appl. 2005; 15(5):1550–9.
36. Hartnett DC, Steuter AA, Hickman RK. Comparative ecology of native and introduced ungulates. In: Knopf FL, Samson F, editors. Ecology and conservation of Great Plains vertebrates. Springer Science and Business Media; 1997. p. 72–102.
37. Koford CB. Prairie Dogs, Whitefaces, and Blue Grama. Wildl Monogr. 1958;(3):3–78.
38. Guenther DA, Detling JK. Observations of cattle use of prairie dog towns. J Range Manag. 2003; 56 (5):410–7.
39. Knowles CJ. Some relationships of black-tailed prairie dogs to livestock grazing. Gt Basin Nat. 1986; 46(2):198–203.

40. Curtin C. Initial results of experimental studies of prairie dogs in arid grasslands: Implications for landscape conservation and the importance of scale. USDA Forest Service Proceedings RMRS-P-40. 2006. p. 57–62.

41. List R, Pacheco J, Ponce E, Sierra-Corona R, Ceballos G. The Janos Biosphere Reserve, Northern Mexico. Int J Wilderness. 2010; 16(2):35–41.

42. IMTA. Extractor Rapido de Informacion Climatica ERIC III. Instituto Mexicano de Tecnologia del Agua; 2008.

43. Holechek BJL, Baker TT, Boren JC, Galt D. Grazing impacts on rangeland vegetation: What we have Learned have positive impacts on rangeland vegetation in arid-to-semiarid areas. Rangelands. 2006; 28(February):7–13.

44. COTECOCA. Coeficientes de agostadero por entidad federativa 1 (Hectáreas/Unidad animal). 2002.

45. Pinedo AC, Hernandez QNS, Melgoza CA, Renteria VM, Velez SVC, Morales NC, et al. Diagnostico actual y sustentabilidad de los pastizales en el estado de Chihuahua ante el cambio climatico. Chihuahua, Mexico; 2013 p. 126.

46. SAGARPA. NORMA Oficial Mexicana NOM-051-ZOO-1995, Trato humanitario en la movilizacion de animales. Diario Oficial de la Federacion. 1998;42–67.

47. SAGARPA. NORMA Oficial Mexicana NOM-062-ZOO-1999, Especificaciones tecnicas para la produccion, cuidado y uso de los animales de laboratorio. Diario Oficial de la Federacion. 2001;107–67.

48. Sikes RS, Gannon WL. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J Mammal. 2011 Feb 16; 92(1):235–53.

49. Peinetti HR, Fredrickson EL, Peters DC, Cibils AF. Foraging behavior of heritage versus recently introduced herbivores on desert landscapes of the American Southwest. Ecosphere. 2011; 2(May):1–14.

50. Laliberte AS, Fredrickson EL, Rango A. Combining decision trees with hierarchical object-oriented Image analysis for mapping arid rangelands. Photogramm Eng Remote Sens. 2007; 73(February):197–207.

51. Ganskopp D, Bohnert D. Do pasture-scale nutritional patterns affect cattle distribution on rangelands? Rangel Ecol Manag. 2006; 59(March):189–96.

52. Augustine DJ, Springer TL. Competition and facilitation between a native and a domestic herbivore: trade-offs between forage quantity and quality. Ecol Appl. 2013 Jun; 23(4):850–63. PMID: 23865235

53. Launchbaughl KL, Howery LD. Understanding landscape use patterns of livestock as consequence of foraging behavior. Rangel Ecol Manag. 2005; 58(2):99–108.

54. Herbel CH, Ares FN, Nelson AB. Grazing Distribution Patterns of Hereford and Santa Gertrudis Cattle on a Southern New Mexico Range. J Range Manag. 1967; 20(5):296–8.

55. Senft RL, Rittenhouse LR, Woodmansee RG. Factors Influencing Patterns of Cattle Grazing Behavior on Shortgrass Steppe. J Range Manag. 1985; 38(1):82–7.

56. Neuenschwander LF, Sharrow SH, Wright HA. Review of tobosa grass (Hilaria mutica). Southwest Nat. 1975; 20(2):255–63.

57. Riegel A. Life history and habits of blue grama. Trans Kansas Acad Sci. 1941; 44:76–85.

58. Howard JL. Salsola kali. Fire Effects Information System, [Online] [Internet]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer); 2014. Available from: http://www.fs.fed.us/database/feis/

59. McCollum ML, Galyean ML, Krysl LJ, Wallace JD. Cattle Grazing Blue Gramma Rangeland I. Seasonal Diets and Rumen Fermentation. J Range Manag. 1985; 38(6):539–43.

60. Fuhlendorf SD, Engle DM. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience. 2001; 51(8):625.

61. O'Meilia ME, Knopf FL, Lewis JC. Some consequences of competition between prairie dogs and beef cattle. J Range Manag. 1982; 35(5):580–5.

62. Derner JD, Detling JK, Antolin MF. Are livestock weight gains affected by black-tailed prairie dogs? Front Ecol Environ. 2006; 4(9):459–64.

63. Cheng E, Ritchie ME. Impacts of simulated livestock grazing on Utah prairie dogs (Cynomys parvidens) in a low productivity ecosystem. Oecologia. 2006 Mar; 147(3):546–55. PMID: 16328551

64. Cid MS, Detling JK, Whicker AD, Brizuela MA. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. J Range Manag. 1991; 44(2):100–5.

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U.S. Fish and Wildlife Service
Region 6
Environmental Contaminants Program

Secondary Lead Poisoning in Golden Eagle and Ferruginous Hawk Chicks Consuming Shot Black-tailed Prairie Dogs, Thunder Basin National Grassland, Wyoming

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Abstract

Recreational shooting of black-tailed prairie dogs (*Cynomys ludovicianus*) is a common activity at Thunder Basin National Grassland (TBNG), Wyoming. The prairie dog carcasses left in the area are scavenged by coyotes (*Canis latrans*), raptors, and other animals. These scavengers are susceptible to lead (Pb) poisoning if they consume Pb bullet fragments or Pb shot when scavenging the shooter-killed prairie dogs. In 2000, a local rehabilitator noted an increase of Pb poisoning cases in raptors (L.Layton, pers. comm. 3/30/01) from the area. We collected several shooter-killed prairie dog carcasses from TBNG for determining if Pb fragments remained embedded in the tissue that potentially would be consumed by raptors. Radiographs showed fragments consistent with Pb to be present. In 2002, we conducted a more in-depth study to determine if Pb poisoning was occurring in raptors at TBNG by documenting the number of raptors on prairie dogs at colonies where shooting occurred, assaying bullet fragments in shot prairie dogs to determine Pb content, and analyzing blood and feather samples of ferruginous hawk (*Buteo regalis*) and golden eagle (*Aquila chrysaetos*) nestlings and feathers from burrowing owls (*Athene cunicularia*) for clinical signs of Pb poisoning.

We observed raptors foraging at prairie dog colonies and collected data on the number of shooters shooting at prairie dog colonies. To determine if raptors preferred foraging on shot prairie dogs, we compared raptor use at prairie dog colonies where shooting occurred to raptor use at prairie dog colonies where shooting did not occur. Shooter intensity did not predict raptor use. We also collected prairie dog carcasses and examined them for Pb shot fragments. We detected metal fragments in four of ten prairie dog carcasses. The total weight of the fragments found in each carcass ranged from 10 – 146 mg. Copper was the primary metal detected in 3 of 4 carcasses; but, significant amounts of Pb (20 mg, 28 mg, and 124 mg) were found in the three carcasses. Blood Pb concentrations in ferruginous hawk nestlings were below sub-clinical levels at TBNG and the control site near Rawlins, Wyoming. Analysis of red blood cell delta-aminolevulinic acid dehydratase activity, hemoglobin levels, and protoporphyrin levels also did not indicate Pb poisoning in ferruginous hawk nestlings. Additionally, blood and feather samples from golden eagle nestlings and feather samples from burrowing owls (juveniles and adults) at TBNG did not indicate Pb poisoning. Although ferruginous hawks and golden eagles (and possibly burrowing owls) scavenge on the carcasses of shot prairie dogs and some carcasses contained Pb-bullet fragments, we did not detect Pb poisoning in any of the birds. Lead poisoning may become important if the availability of alternate food sources decreases or shooter intensity increases.

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INTRODUCTION

The Thunder Basin National Grassland (TBNG), managed by the U.S. Forest Service (USFS), is located 40 miles north of Douglas, Wyoming. TBNG provides habitat for white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), and numerous small mammals. There are 6,177 ha of black-tailed prairie dog (*Cynomys ludovicianus*) towns, of which 1,388 are managed as retention areas (where no control activities occur) at TBNG. The remaining 4,788 ha can have prairie dog control activities, which include shooting or poisoning using zinc phosphide (USFS and BLM 1992).

The prairie dog colonies serve as a locally important food source for raptors. Golden eagles (*Aquila chrysaetos*) and ferruginous hawks (*Buteo regalis*) nest on TBNG. Approximately 100 bald eagles (*Haliaeetus leucocephalus*) use the area for winter roosting, and feed on prairie dogs and winter-kill animals. Golden eagles also feed on winter-kill animals; and in the summer, golden eagles and ferruginous hawks feed on shooter-killed prairie dogs almost exclusively (Tim Byer, USFS, pers. comm. 5/25/00). Annual use by prairie dog-shooters of TBNG ranges from 8,000 to 8,500 shooter-use-days. Prairie dog shooters do not collect the prairie dog carcasses resulting in an easy food resource for the raptors.

As a result of scavenging on shooter-killed prairie dogs, raptors may be exposed to chronic lead (Pb) concentrations by ingesting Pb pellets or Pb-core bullet fragments that are embedded in the tissues of the prairie dog carcasses. Although raptors often regurgitate bones, feathers or fur, and other foreign objects, Redig et al. (1980) found that Pb is not necessarily incorporated into castings and can be retained in the gastrointestinal tract resulting in Pb poisoning. In 2000, several golden eagles with suspected Pb poisoning were brought to a rehabilitator in nearby Casper, Wyoming (L. Layton, raptor rehabilitator, pers. comm. 3/30/01). These cases raised questions about the impacts of recreational shooting on birds of prey.

There is sufficient documentation of raptors being poisoned from ingesting Pb shot in waterfowl tissues (Benson et al. 1974; Jacobsen et al. 1977); but, documentation of Pb poisoning in raptors that consume shooter-killed small mammals is more limited (Locke et al. 1969; Pattee et al. 1981). Even so, it is possible for raptors to suffer from Pb poisoning after consuming small mammal carcasses containing Pb shot or fragments. For example, an Andean condor (*Vultur gryphus*) was poisoned after eating shooter-killed rabbits and ground squirrels (Locke et al. 1969). In the spring of 2000, three reintroduced California condors (*Gymnogyps californianus*) were found dead in Arizona as a result of Pb poisoning and two other were being treated (USFWS 2000). One of the condors had 17 Pb shotgun pellets in its digestive system. Another study conducted on wintering bald eagles in a Utah desert, found that eagles consuming shooter-killed jackrabbits ingested Pb shot and bullet fragments (Platt 1976). Furthermore, a report by Craig et al. (1990) reported that 10 of 17 golden eagles and seven of eight bald eagles that they found in Idaho were exposed to Pb. One of the golden eagles contained a fragment from a copper-jacketed Pb bullet. The authors stated their sample was biased because they sampled only sick and dead birds, but they believe that Pb poisoning may be a more serious problem in golden eagles than originally identified. Finally, the U.S. Fish and Wildlife Service (1986) reported that shooter-killed jackrabbits consumed by bald eagles from the Great Plains, the High Plains of Texas, and the Black Hills of South Dakota may constitute a major source of Pb to these raptors.

Birds suffering from Pb poisoning are often weak and may ultimately die from another cause such as predation, disease, or starvation (Jacobsen et al. 1977). In a study by Pattee et al. (1981), five bald eagles were dosed with #4 Pb shot. Four of the five birds died and the stomach of each bird contained at least one Pb shot at the time of death. The fifth eagle survived but went blind and was eventually sacrificed. The individual response of the eagles to Pb shot was variable and probably the result of the interaction of various factors such as the number of shot retained, amount of Pb eroded, and individual susceptibility (e.g., health, age).

Lead is typically not transferred from the adults to the young through egg-laying (Pattee 1984). However, young can ingest Pb pellets or fragments embedded in the tissue of food brought to the nest by the parents. Hoffman et al. (1985a) reports that nestlings of kestrels and other altricial birds, such as eagles, exposed to Pb are expected to be impacted to a greater degree (e.g. impaired survival and growth) than precocial species, such as mallards (*Anas platyrhynchos*), because of the delay in development and growth.

Raptors can be evaluated for Pb poisoning using non-lethal means by collecting blood samples. General guidelines, based on associated physiological effects, exist to categorize Pb concentrations in whole blood samples from Falconiformes (Franson 1996). Additionally, the activity of δ-aminolevulinic acid dehydratase (ALAD) in erythrocytes, one of several enzymes necessary for heme synthesis, can be measured to determine exposure to Pb (Leonzio and Fossi 1994). Lead inhibits the activity of this enzyme (Pain 1996) and blood Pb concentrations are directly correlated with ALAD inhibition (Mayer et al. 1992). The use of ALAD in raptors exposed to Pb is documented (Franson et al. 1983; Hoffman et al. 1985a; and Hoffman et al. 1985b) and has become a standard technique in diagnosing Pb poisoning in birds (Leonzio and Fossi 1994, Pain 1995, Henny et al. 2000). Over-exposure to Pb is also known to cause reduced total-blood hemoglobin concentration, elevated levels of protoporphyrin, and decreased packed cell volume (PCV) (Franson 1986; Pain 1995).

To determine if eagles and ferruginous hawks at TBNG are being impacted by ingesting Pb shot from prairie dog carcasses, we established the following objectives: 1) Quantify raptor activities (including feeding, resting, landing) on hunted and non-hunted prairie dog towns on TBNG; 2) Radiograph a random sample of shooter-killed prairie dogs for the presence of Pb pellets/bullet fragments and assay recovered fragments for Pb verification; and, 3) Obtain blood and feathers from nestling raptors feeding on shooter-killed prairie dogs for Pb concentrations and comparison with nestlings not feeding on shooter-killed dietary items.

METHODS

Study Sites

TBNG was selected as the treatment site (Figure 1) due to heavy use of the area for recreational prairie dog shooting. It is administered as part of the Medicine Bow National Forest by the USFS and is located in northeast Wyoming within Campbell, Weston, Converse, and Niobrara counties. TBNG covers 231,488 ha of National Forest System land intermingled with Bureau of Land Management (BLM), State, and private lands. The topography is characterized by moderately level plains, rolling hills, and steep escarpments. Precipitation is <30 cm/year and elevation ranges from 1,370 to 1,600 m. The dominant vegetation is Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), needle-and-thread grass (*Stipa comata*), blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), ponderosa pine (*Pinus ponderosa*), and cottonwood (*Populus* spp.) corridors.

The reference site, located in south central Wyoming near Rawlins (Figure 1), is characterized as a high, cool desert with <30 cm of precipitation/year and an elevation ranging from 1,829 to 2,134 m. Sagebrush communities are the most common type of vegetation. Other assorted community types are interspersed throughout the landscape including sagebrush/mountain shrub, saltbush steppe, greasewood lowlands and badlands.

Raptor Use of Prairie Dog Colonies

We monitored eight prairie dog colonies in TBNG during six observation periods, including colonies where shooting did not occur. Observation periods lasted three hours and we recorded raptor activity at 10-minute intervals and included the amount of time raptors hunted, fed, or rested in the area. Observations were distributed during the day so that two observations were performed between 0700 and 1100 hrs, 1101 and 1400 hrs, and 1401 and 1800 hrs. Observations occurred between June 7 and July 20, 2002 and were randomly distributed. Shooter intensity was estimated from information collected from voluntary surveys at each colony. Shooters were interviewed and the information on gun caliber and bullet types used for shooting was recorded. Simple linear regression was used to determine if raptor use was predicted by shooter hours and colony size. This information was required to document the extensive and almost exclusive use of the shooter-killed prairie dogs as a primary food source for raptors on TBNG.

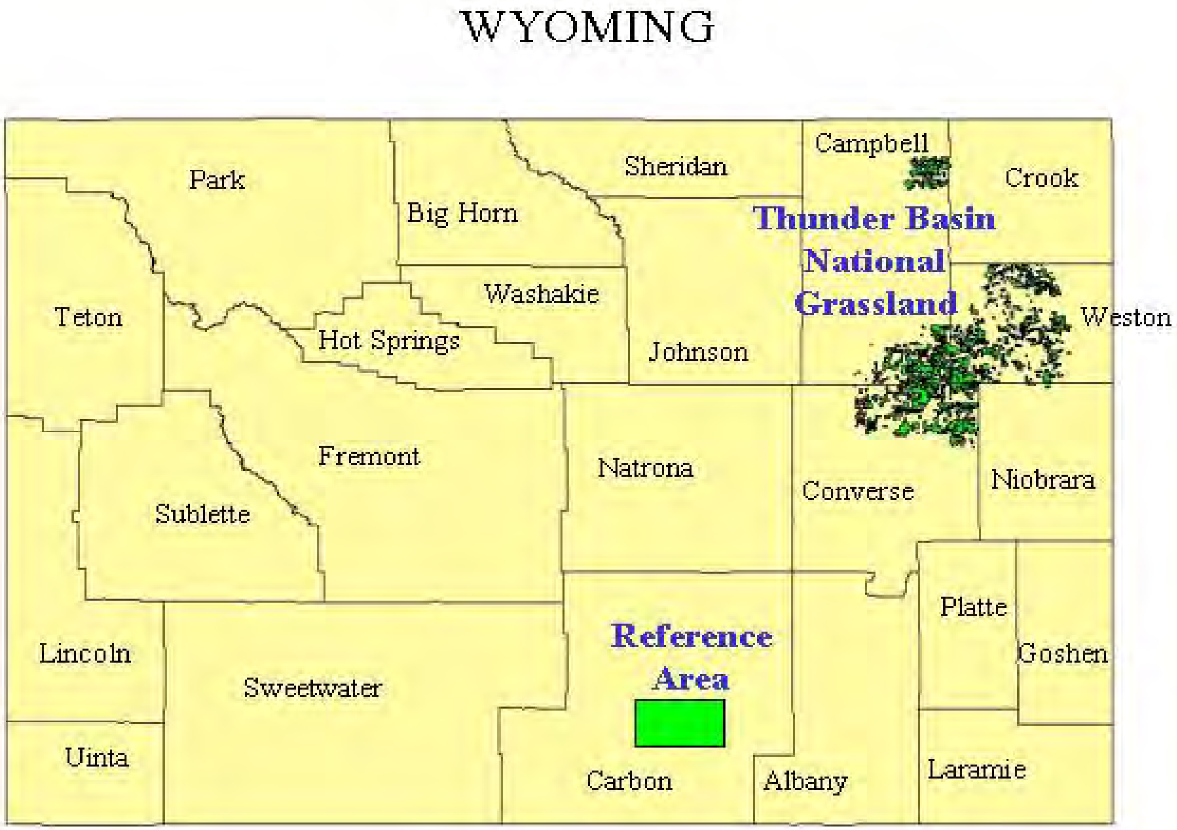


Figure 1. Location of Thunder Basin National Grassland and the reference area in Wyoming.

Bullet Fragments in Prairie Dog Carcasses

As a preliminary investigation to demonstrate that most ammunition used to shoot prairie dogs does not exit the carcasses but rather is retained in fragments, USFWS personnel collected 22 prairie dog carcasses during July 2000 at TBNG. The carcasses were radiographed at the Wyoming State Vet Laboratory (WSVL) to demonstrate that bullet fragments were contained in the tissue. Funding was not available to analyze the content of the fragments from these carcasses. In 2002, ten additional prairie dog carcasses were collected and radiographed by WSVL for the presence of bullet fragments. The metal fragments were removed from the carcasses and assayed by digestion in HNO_3 and H_2O_2, diluted and analyzed on an Elan 6100 Inductively Coupled Plasma-Mass Spectrometry (ICP-MS; Perkin Elmer, Norwalk, CN) at the WSVL, according to their Standard Operating Procedure (WSVL 3/21/01).

Blood and Feather Sampling

The USFS has monitored nesting success of golden eagles and ferruginous hawks on TBNG each year since 1981 (USFS and BLM 1992). There are currently 30 active golden eagle nests and 25 ferruginous hawk nests at TBNG. We also used information from coal mines to locate active nests at nearby mining sites. Other nests were located using information obtained from Thunder Bird Wildlife Consulting (Wright, WY) and by locating undocumented nest sites. We monitored egg-laying twice weekly from February 2002 until July 2002 when fledgling occurred. Nests were observed through binoculars to reduce disturbance and stress to the birds.

Reference values for Pb concentrations in blood and ALAD levels in raptors is scarce, so samples from ferruginous hawks nesting on platforms on BLM land in south central Wyoming were obtained. The BLM has monitored nest success and productivity of the ferruginous hawk nests for several years. Shooting of prairie dogs does not occur in this area and the raptors' primary diet consists of ground squirrels. We were not able to obtain any golden eagle nestlings for reference birds.

Once nestlings were old enough (approximately 20 d), we collected blood for five hematological analyses, which included blood-Pb concentration, ALAD activity, hemoglobin levels, protoporphyrin levels, and packed cell volume (PCV). PCV readings are required for ALAD analysis. To collect a blood sample, the brachial artery of the nestling was swabbed with alcohol. Two milliliters of blood was obtained using a 25-gauge needle syringe containing heparin-treated beads (USFWS 1996). Immediately after the syringe was removed from the puncture site, we used a heparinized capillary tube to collect blood for measuring PCV. Pressure was applied to the puncture site until bleeding stopped. The nestlings were weighed, and the length of the 8th primary and the width of the footpad were measured to determine age and sex. We collected some chest pin feathers and placed them resealable bags. Down feathers were collected from nestlings that had not developed pin feathers at the time of sampling. We placed migratory bird identification and Wyoming state bands on their legs and returned the nestlings to their nest.

Samples in capillary tubes were spun by micro-centrifuge for 3 min. The PCV was calculated as the ratio between the hemoglobin of the whole blood and the hemoglobin of packed red blood cells with all plasma removed. For the remaining sample, we divided the 2.0 ml of blood into four sterile heparinized cryogenic vials, each containing a 0.5-ml aliquot of blood. Samples for Pb concentration, hemoglobin, and ALAD were immediately placed into liquid nitrogen and frozen.

Blood Pb analysis, including analysis for percent moisture, was performed at the University of Wyoming Red Buttes Environmental Biology Laboratory (RBEBL; Laramie, WY) on a Varian SpectrAA600 graphite furnace atomic absorption spectrophotometer equipped with Zeeman background correction (Fernandez and Hilligoss 1982). An unused syringe was also analyzed to ensure no external contamination was present.

Hemoglobin analyses were conducted at Antech Diagnostic (Irvine, CA) by the cyanmethomoglobin method and spectrophotometric measurement (Sari et al. 2001). ALAD activity was measured colorimetrically by the National Wildlife Health Center (Madison, WI) with a Beckman DU-65 (Beckman Instruments, Fullerton, CA) spectrophotometer, based on methods described by Burch and Siegel (1971). ALAD activity was determined with duplicate 0.1-ml aliquots of blood; the results reported are the mean of the duplicates. One unit of enzyme activity is defined as an increase in absorbance at 555 nm of 0.100, with a 1.0-cm light path/ml of erythrocytes/hour at 38° C. Protoporphyrin levels were measured with a hematofluorometer at 2 h, 24 h, and 48 h after blood collection according to Franson et al. (1996).

For Pb analysis in feathers, the feathers were washed vigorously in 50% aqueous acetone, followed by three rinses with deionized water to remove loosely adherent external contamination. After washing, feathers were air dried overnight at 60° C and weighed to the nearest 0.1 mg. Weighed samples were digested at 180° C for 10 min. with a combination of 0.5-ml each H_2O_2 and HNO_3 in a microwave digestion system (MDS 2000, CEM Corp, Mathews, NC), cooled, and diluted to 5 ml with deionized water. The diluted samples were analyzed together with appropriate standards, reference samples, and Pb-spiked duplicates by ICP-MS at the WSVL.

Because the opportunity arose, we also analyzed feathers from burrowing owls located at TBNG. Sarah Lantz, with the University of Wyoming, was conducting unrelated research on burrowing owls and collected chest pin feathers from owls that foraged at prairie dog colonies subjected and not subjected to Pb shot at TBNG. Burrowing owls were located with standardized call-broadcast surveys, and captured with two-way traps and baited spring traps.

For data analysis, if Pb concentrations were below the instrument's detection limit (0.001 ppm), the median of the detection limit and zero was used as an individual Pb concentration. Blood Pb concentrations were compared and classified with baseline levels and ranges in Falconiformes as established by Franson (1996).

Statistical Analysis

Ninety-five percent confidence intervals and graphs were created using Sigma Plot (version 7.0). Pearson correlation coefficients were calculated using Systat (version 10..2) to determine if correlation existed between blood Pb concentrations and feather Pb concentrations.

RESULTS

Raptor Use of Prairie Dog Colonies

During 144 h of observations, ferruginous hawks (0.36/hr), golden eagles (0.34/hr), turkey vultures (0.27/hr; *Cathartes aura*), red-tailed hawks (0.09/hr; *Buteo jamaicensis*), American kestrels (0.05/hr; *Falco sparverius*), prairie falcons (0.02/hr; *Falco mexanicus*), and Swainson's hawks (0.02/hr; *Buteo swainsoni*) were observed either flying or perched at prairie dog colonies (Table 1; Appendix 1). We did not observe any of the raptors feeding on prairie dog carcasses. Shooter hours (n = 8; r^2 = 0.2%; P = 0.921) and colony size (n = 8; r^2 = 0.3%; P = 0.894) were not predictors of raptor use.

Table 1. Number of ferruginous hawks (FeHa) and golden eagles (GoEa) using black-tailed prairie dog colonies in Thunder Basin National Grasslands, Wyoming, during June and July, 2002.

Prairie Dog Colony	Size of Prairie Dog Colony (ha)	Shooter Hours	Number of FeHa and GoEa Observed	Number of All Raptors Observed
Teckla	42	4	36	41
Reservoir Dogs	17	11.5	18	21
Big Steckley	121.3	63	4	28
Little Steckley	15.8	0	5	6
450 East	12.5	17	1	4
BT450	89	72.5	19	31
Mackey	27.4	2	9	17
Rochelle Hills	23.8	2	7	16

Bullet Fragments in Prairie Dog Carcasses

The objective was to collect fifty shooter-killed prairie dogs during June 2002 but only ten prairie dog carcasses could be salvaged as prairie dog populations were low and shooter activity was minimal compared to other years. We found bullet fragments in four of 10 carcasses (Table 2; Appendix 2a). The total weight of the bullet fragments recovered from each carcass was 92.5 ± 60.7 mg (Mean ± SD; *n* = 4). Significant amounts of Pb were in three carcasses.. Copper was the primary metal ($\geq$78%) in three samples and was accompanied by traces of zinc. Funding was not available to analyze the fragments from the 22 carcasses collected during the preliminary investigation in July 2000. However, of the 22 prairie dog carcasses, 19 had fragments that were consistent with Pb (Appendix 2b and 2c).

Table 2. Assay results for lead (Pb), copper (Cu), and zinc (Zn) of bullet fragments recovered from black-tailed prairie dog carcasses collected from Thunder Basin National Grasslands, Wyoming, July, 2002.

Sample	Rifle Caliber	Total Shot Weight (mg)	Pb Content %[a]	Pb Content mg	Cu Content %[a]	Cu Content mg	Zn Content %[a]
1	0.22-250	146	19	28	78	113	<1
2	0.22-250	10	<1	---	106	10	<1
3	0.25-06	85	23	20	79	67	<1
4	0.25-06	129	96	124	<1	---	<1

[a] Given the very high concentrations of Pb and Cu, the samples had to be repeatedly diluted in order to estimate the percentages of each metal; thus the numbers do not add up to exactly 100%.

Blood and Feather Analysis

Twenty three ferruginous hawk nestlings (26.5 ± 3.2 days old) (Appendices 3a and 3b) were sampled for blood and feather samples at nine nests in TBNG. We also collected seven blood samples and six feather samples from seven golden eagle nestlings in TBNG. At the control site near Rawlins, blood and feather samples were collected from 23 ferruginous hawks nestlings (39.2 ± 2.8 days old) at nine nests (Appendices 3a and 3b).

Ferruginous hawk (0.021 – 0.061 µg Pb/g wet weight (ww) at TBNG; 0.023 – 0.167 µg Pb/g ww at Rawlins) and golden eagle (0.03 – 0.074 µg Pb/g ww at TBNG) blood samples were below sub-clinical levels (Franson 1996) of 0.2 to 1.5 µg Pb/g ww (Figure 2; Appendix 3c). The ALAD activity (215 – 460 Burch & Siegel units), hemoglobin levels (5.5 – 15.9 units), and protoporphyrin levels (5 – 34 units at 48h) in ferruginous hawk nestlings at TBNG also suggested against Pb poisoning (Figure 3; Appendices 3c and 3d) and were not significantly different from the ALAD activity (242 – 339 Burch & Siegel units), hemoglobin levels (9.1 –

15.3 units), and protoporphyrin levels (6 – 17 units at 48h) in ferruginous hawk nestlings at the Rawlins site. However, PCV in ferruginous hawk nestlings was higher at the Rawlins sute (35.17 – 37.25) than in TBNG (29.13 – 31.75). The 95% confidence intervals for the other hematological parameters in blood samples from the golden eagles were as follows: ALAD activity = 404.3 – 528.5, protoporphyrin levels at 48 h = -7.2 – 79.0, hemoglobin levels = 7.87 – 11.59, and PCV = 25.46 – 35.1.

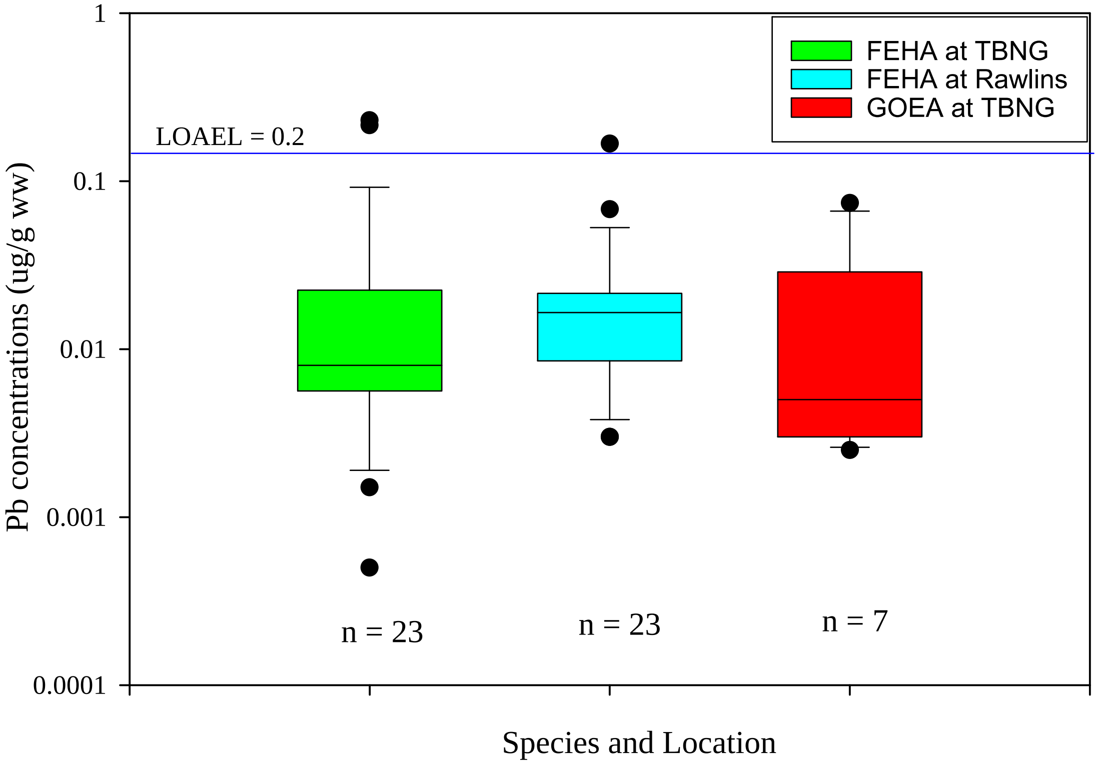


Figure 2. Range and median blood lead (Pb) concentrations (µg/g wet weight (ww)) in golden eagles (GOEA) and ferruginous hawks (FEHA) from Thunder Basin National Grassland (TBNG) and the reference site (Rawlins), Wyoming, July 2002. The lowest observed adverse effect level (LOAEL) is 0.2 ug/g ww.

Pb concentrations in feathers of ferruginous hawk nestlings from TBNG ranged from 0.08 – 24.72 µg/g for pin feathers and 0.183 – 1.306 µg/g for down feathers. At the reference site, all pin feathers were collected from ferruginous hawk nestlings with Pb concentrations ranging from 0.048 – 2.616 µg/g (Figure 4; Appendix 3e). Pin feathers from golden eagle nestlings on TBNG had Pb concentrations ranging from 0.101 to 1.935 µg Pb/g. The one and only down feather sample collected from a golden eagle nestling on TBNG had the highest Pb concentration (1,070 µg Pb/g) of all feathers from raptors collected (Figure 4; Appendix 3e).

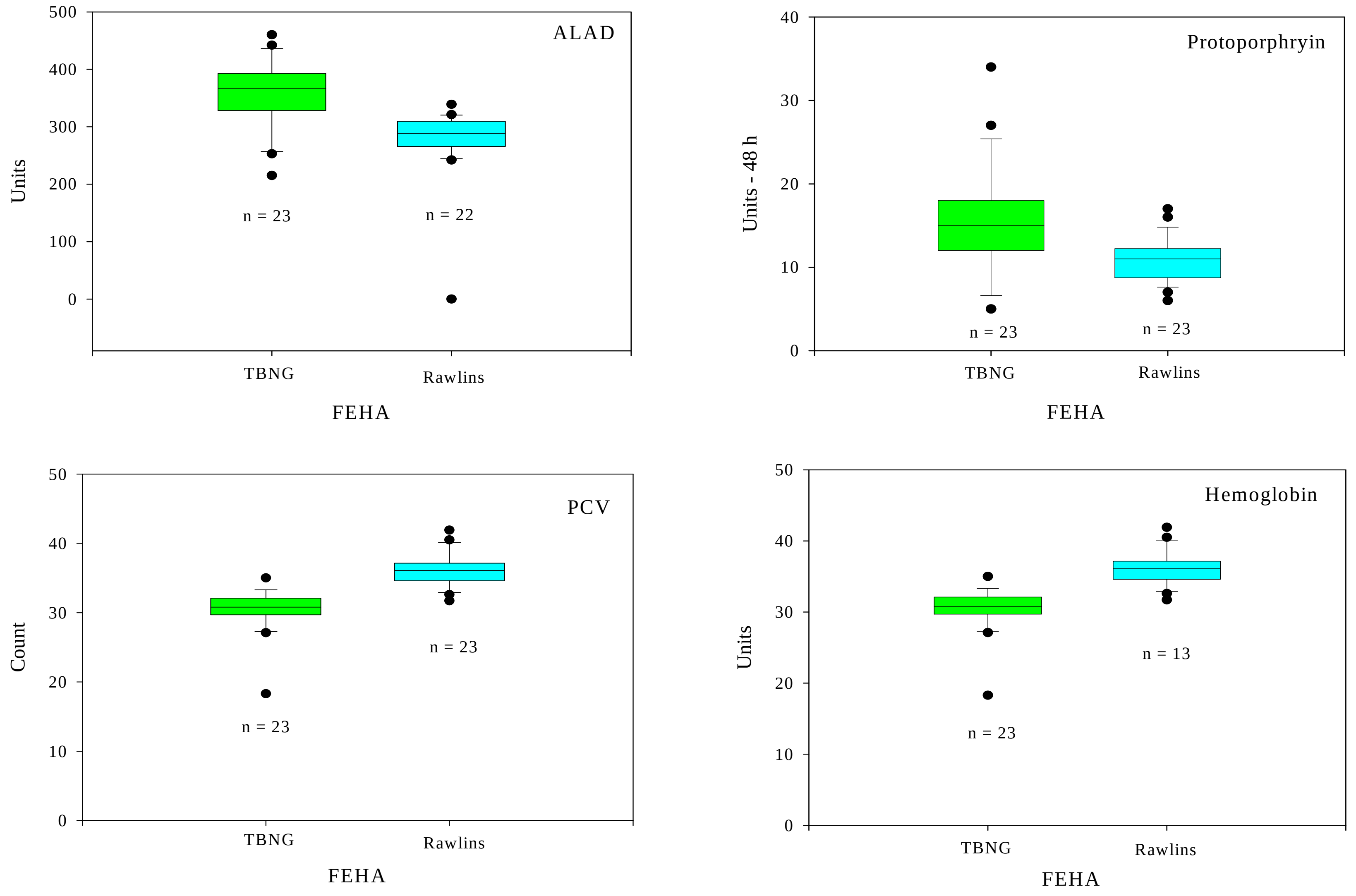


Figure 3. Range and median of blood parameters in ferruginous hawks (FEHA) from Thunder Basin National Grassland (TBNG) and the reference site (Rawlins), Wyoming, July 2002.

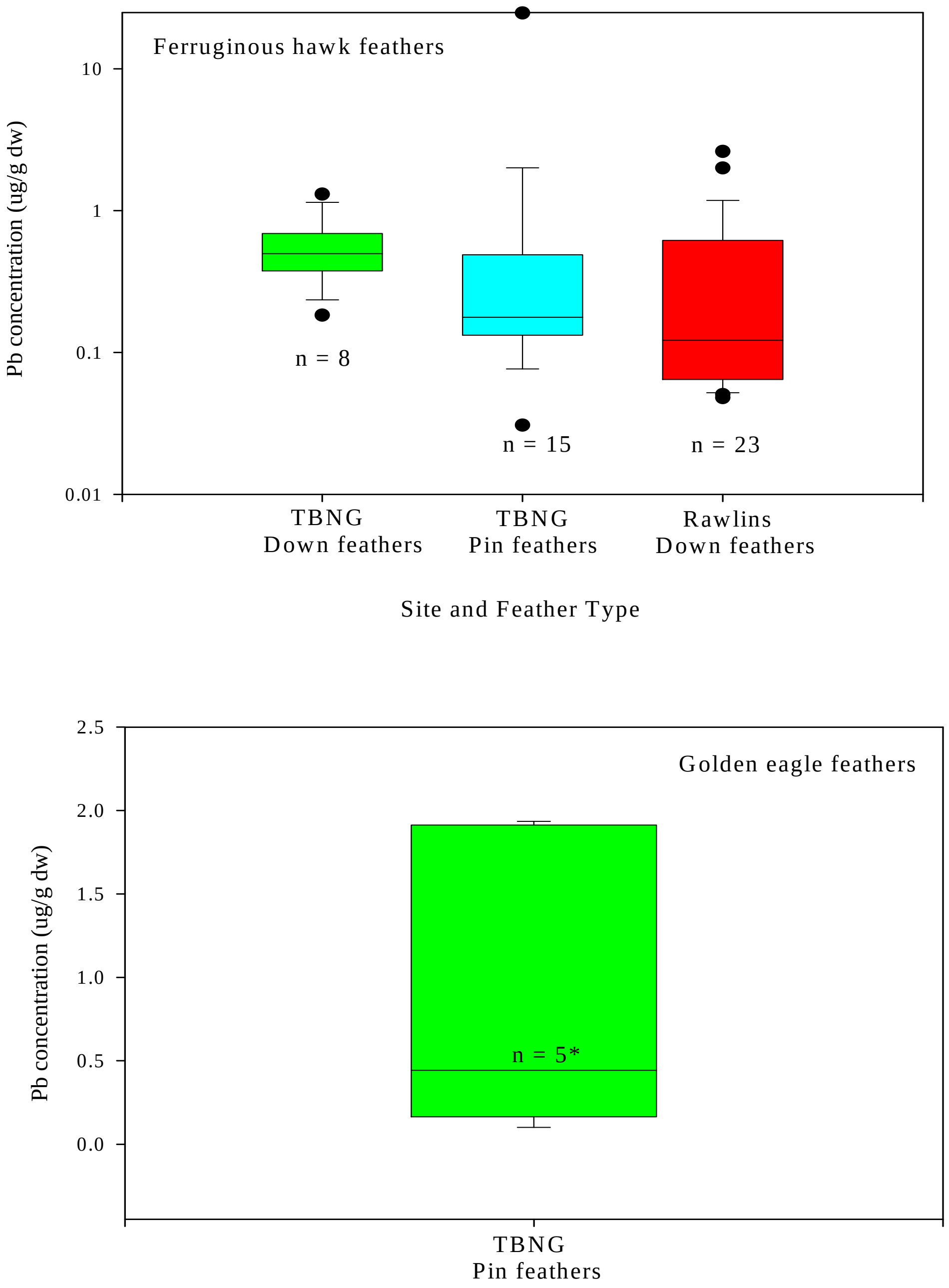
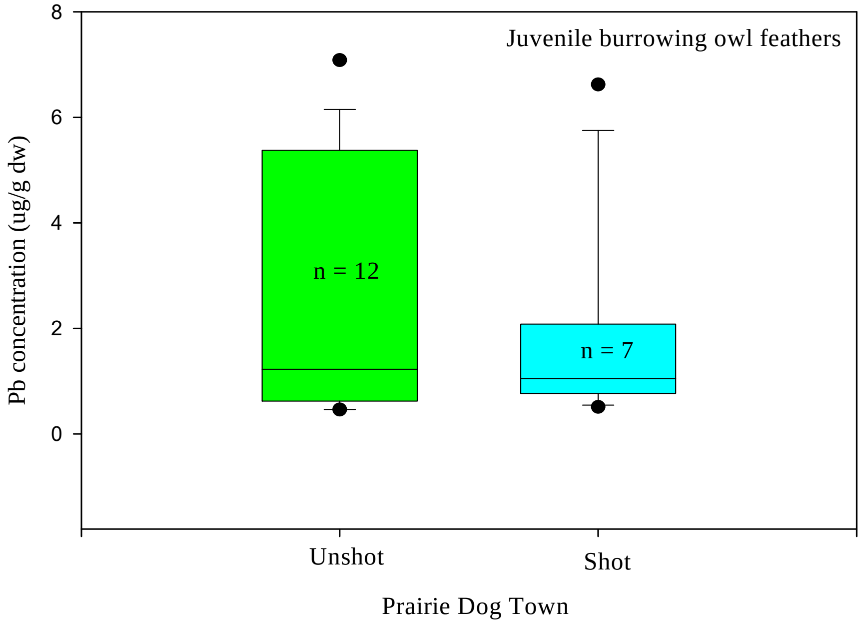


Figure 4. Range and median lead (Pb) concentrations in ferruginous hawk (FEHA) and golden eagle (GOEA) nestling feathers from Thunder Basin National Grassland (TBNG) and the reference site (Rawlins), Wyoming, July 2002. The one down feather collected from the golden eagle nestling with a Pb concentration of 1, 070 ug Pb/g is not shown graphically.

Chest pin feathers from 43 burrowing owls, 20 from shot prairie dog colonies [7 juvenile/13 adult] and 23 from unshot prairie dog colonies [12 juvenile/11 adult]) in TBNG, were also low in Pb and there was no statistical difference in feathers of owls collected on shot or unshot prairie dog towns (Figure 5; Appendices 3f and 3g).



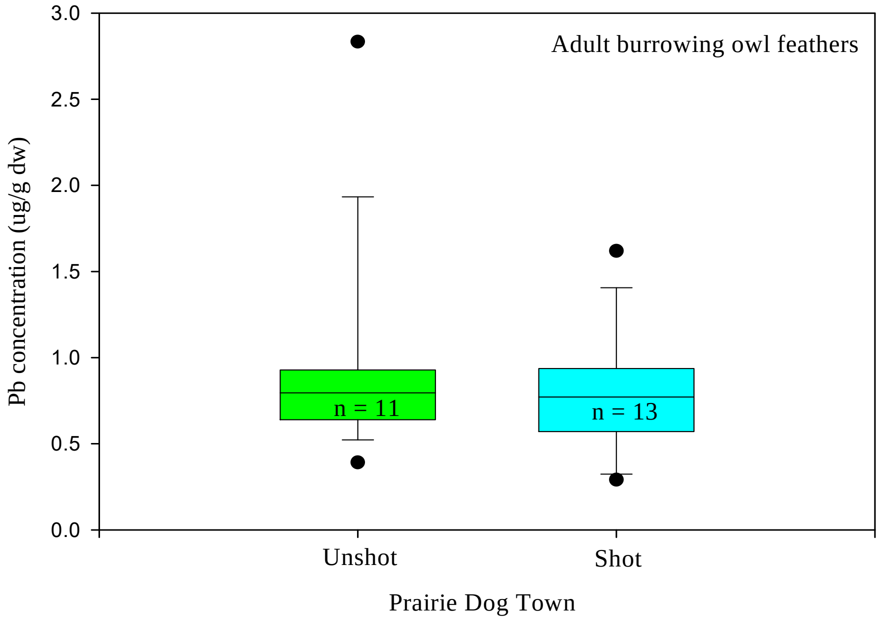


Figure 5. Range and median lead (Pb) concentrations in feathers from adult and juvenile burrowing owls from Thunder Basin National Grassland (TBNG), Wyoming, July 2002.

Chest pin feathers of juvenile burrowing owls ranged from 0.512 to 2.27 ug Pb /g at shot prairie dog towns and from 0.46 – 7.08 ug Pb/g at unshot prairie dog towns. Adults had lower ranges of Pb concentrations in their feathers than juveniles from both shot (0.291 – 1.62 ug Pb/g) and unshot shot prairie dog towns (0.391 – 2.83 ug Pb/g). Differences in Pb concentrations in feathers, however, were not significantly different between adult and juvenile feathers ($p = 0.07$; $p = 0$).

DISCUSSION

Raptor Use of Prairie Dog Colonies

We observed ferruginous hawks and golden eagles hunting and foraging at prairie dog colonies but did not observe them scavenging on shot prairie dogs. A sylvatic plague (*Yersinia pestis*) outbreak had drastically reduced prairie dog numbers at many of the colonies in TBNG during 2001-2002 (T. Byer, USFS, pers. comm. 10/31/01) and may explain, in part, why we did not observe any raptors scavenging on shooter-killed prairie dogs. Furthermore, raptor use did not increase as shooting intensity increased or as the colony size increased as we had predicted. This may be explained because there was an increase in the availability of alternate prey species (in addition to a reduction in the number of prairie dogs due to the sylvatic plague outbreak). Long-term surveys in this area indicated that Lagomorph numbers were increasing (Clayton 2001). Because Lagomorphs were relatively abundant, foraging and scavenging at prairie dog colonies may have been less likely. However, it is well documented that raptors will scavenge carcasses such as shooter-killed jackrabbits (Platt 1976), deer, and other animals (Craig et al. 1990; Bechard and Schmutz 1995). Further investigation may be warranted to determine if raptors are ingesting Pb fragments from shooter-killed prairie dogs once prairie dog populations rebound, Lagomorph populations decline, and the raptors return to an-almost-exclusive diet of shooter-killed prairie dogs.

Bullet Fragments in Prairie Dog Carcasses

We found Pb fragments in three of the prairie dog carcasses examined. Although it is not possible to assess if Pb toxicity would have occurred in the raptors at TBNG if those carcasses were scavenged, the results of the Pb fragments excised from the prairie dog carcasses, as well as the radiographs show that Pb in shooter-killed prairie dogs is available and the potential for ingestion by scavengers, including raptors, is present.

Factors that can affect the toxicity of Pb if ingested by raptors include the health of the bird at the time of ingestion, amount and frequency of Pb ingestion, and whether Pb pieces are ingested or regurgitated as a casting. Miller et al. (2000) reported that although 9% of golden eagles and bald eagles sampled in Saskatchewan, Canada ingested shotshell pellets from scavenging dead waterfowl, regurgitated castings (<2%) contained Pb shotshell pellets. However, Redig et al. (1980) found that Pb fragments that are consumed are not necessarily incorporated into regurgitated castings and can be retained in the gastrointestinal tract resulting in Pb poisoning. In particular, bald eagles do not regularly regurgitate castings, which can result in longer retention of Pb pellets and more susceptibility to Pb poisoning (Redig et al. 1980).

Furthermore, adult raptors feed their nestlings the prime tissues of scavenged carcasses (Pattee 1984), which tend to contain the greater amount of shot, potentially exposing the young to greater amounts of Pb. In addition to this increased risk, poisoning caused by ingestion of food items containing Pb has greater impacts on nestlings of various altricial birds, such as American kestrels, golden eagles and ferruginous hawks, than adults (Hoffman et al. 1985b). Such impacts on nestlings include mortality, reduced growth, and pronounced hematological effects (Hoffman et al. 1985b). We did not have any nestlings that succumbed to the toxic effects of Pb and we do not know for certain if any of the nestlings we observed actually ingested Pb, but as little as one Pb shot in waterfowl, if ingested, can cause acute or chronic toxicity effects, with chronic effects not often noticeable at first (Wobeser 1981).

Based on our recovery and analysis of bullet fragments from four of the ten carcasses, copper appeared to be the metal most consumed by scavenging raptors. Approximately 113 mg, 10 mg, and 67 mg of copper were found in three carcasses. However, we did not analyze copper concentrations in blood and found little information in our literature review of copper toxicity in raptors. More research is needed on copper poisoning in raptors.

Blood and Feather Analysis

Blood Pb concentrations in all ferruginous hawks and golden eagles sampled were well below sub-clinical levels of 0.2 to 1.5 μg Pb/g wet weight (Franson 1996) except for the occasional outlier. 'Sub-clinical' is indicative of potential physiological injury from which the bird would probably recover if Pb exposure was terminated (Franson 1996). The levels that we detected indicate Pb is present in the environment but at low levels. Additionally, comparisons of ALAD activity, protoporphyrin levels, and hemoglobin levels between ferruginous hawks at control and treatment sites indicate that Pb poisoning was not occurring in raptors in TBNG. However, PCV of nestlings at TBNG was significantly lower than at the control site. It is likely that PCV was lower at TBNG because of nestling age differences. The average age of nestlings sampled in Rawlins and TBNG was 39.2 and 26.5 days old, respectively. PCV increases in young animals with age to fulfill the increasing metabolic demands for oxygen associated with increasing body size (Rawson et al. 1992).

Analysis of nestling ferruginous hawk and golden eagle feathers for Pb concentrations was conducted with the purpose of having an additional measure of Pb poisoning for this study According to Burger (1993), concentrations of metals incorporated into feathers reflect concentrations of metals in the blood at the time of feather formation. The metals concentrations therefore, represent current dietary exposure and metals mobilized from internal organs. For juvenile birds that have not undergone a migration, the metal concentrations in their feathers represent the exposure to metals at a given location (Burger 1993; Golden et al. 2003).

However, some feather Pb concentrations in our samples were much higher than others, which did not correlate with the respective blood analyses. Examples of this include: 1) a golden eagle that had a feather Pb concentration of 1,070 μg Pb/g and a blood Pb concentration of only 0.035 μg Pb/g and 2) a ferruginous hawk that had a feather Pb concentration of 24.7 μg Pb/g and a blood Pb concentration of only 0.023 μg Pb/g. Burger and Gochfeld (2000) reported that tissue type is the strongest contributor responsible for the variation in concentrations of metals, with Pb concentrations highest in feathers. Even though Pb concentrations are known to be highest in feathers, we were unsure how to interpret such large discrepancies. Additionally, there were no reference values for Pb concentration in feathers of Falconiformes available in the scientific literature to indicate a Pb poisoning threshold; although, metal levels in blood represent short-term exposure while feather metal levels represent longer, chronic body burdens (during the last molt) (Evers et al. 2005).

If Pb poisoning was occurring in raptors at TBNG from scavenging shot prairie dogs, there are several reasons why it was undetectable. First, the plague severely reduced prairie dog numbers in 2001-2002. Second, 13% of TBNG was closed to prairie dog shooting in an effort to reintroduce black-footed ferrets. Increased regulations on shooting and decreased numbers of prairie dogs contributed to a decrease in the number of shooters visiting TBNG during the course of our study. Finally, long-term surveys in this area indicate that Lagomorphs were very abundant, thus, the likelihood of birds of prey scavenging shot prairie dogs during our study may have been reduced.

Even though we did not detect Pb poisoning at TBNG, our results confirm that some carcasses of shot prairie dogs contain Pb fragments and scavenging could result in Pb poisoning. The frequency with which it occurs is likely to be uncommon and dependent on other factors such as prairie dog numbers, shooter intensity, availability of alternate food sources, and regulations on shooting.

A repeat of this unique study would be beneficial in determining if an increase in shooting pressure on prairie dogs would result in an increase in the abundance of raptors feeding on prairie dog carrion and subsequently an increase in blood Pb concentrations in the raptors. Golden eagle populations in Wyoming are declining (Wyoming Game and Fish Dept. 1995) and the ferruginous hawk is considered a sensitive species by the USFS. The bald eagle may be delisted from the Threatened and Endangered Species list in the near future but numerous threats still remain to these birds including Pb poisoning. Additionally, a more in-depth study would allow us to collect data on potential impacts to raptors associated with the ingestion of copper fragments embedded in shooter-killed prairie dogs. Obtaining additional feather samples from juvenile raptors would be beneficial for examining differences in metal concentrations between pin feathers and down feathers. Correlations between metal concentrations in blood and feathers would be better defined with additional sampling of raptors at TBNG. Sampling both juvenile and adult ferruginous hawks, golden eagles, and burrowing owls would be beneficial for determining differences in metal concentrations among species and to determine if age-related differences exist in the accumulation of Pb.

Acknowledgments–The authors thank the U.S. Fish and Wildlife Service, Wyoming Game and Fish Department, and Wyoming Cooperative Fish and Wildlife Research Unit for funding this research. Additionally, the following individuals made significant contributions to this study: L. Apple, T. Byer, K. Clayton, C. J. Boese, C. Franson, K. Gordon, K. Keffer, S. Lantz, C. Lockman, J. S. Meyer, M. Raisbeck, and R. Siemion. Finally, we thank K. Munney and D. Major of the U.S. Fish and Wildlife Service, J. Meyer of the University of Wyoming, and two anonymous reviewers for their comments in improving the manuscript. Capture and handling protocols were reviewed and approved under the University of Wyoming Animal Care and Use Committee Form number A-3216-01.

REFERENCES

Bechard, M.J. and J.K. Schmutz. 1995. Ferruginous hawk (*Buteo regalis*). In: A. Poole and F. Gill, eds. *The Birds of North America, No. 172*. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C. 20 pp.

Benson, W.W., B. Pharaoh, and P. Miller. 1974. Lead poisoning in a bird of prey. Bull. Environ. Contam. Toxicol. 11: 105-108.

Burch, H.B. and A.L. Siegel. 1971. Improved method for measurement of delta-aminolevulinic acid dehydratase activity of human erythrocytes. Clin. Chem. 17: 1038-1041.

Burger, J. 1993. Metals in avian feathers: Bioindicators of environmental pollution. Rev. Environ. Toxicol. 5: 203-311.

Burger, J. and M. Gochfeld. 2000. Metals in Laysan albatrosses from Midway Atoll. Arch. Environ. Contam. Toxicol. 38: 254-259.

Clayton, K.M. 2001. Raptor ecology in the Thunder Basin of northeast Wyoming. Thunder Basin Grasslands Prairie Ecosystem Association Technical Bulletin Number 1: The History, Ecology, and Economy of the Thunder Basin Prairie Grasslands: Building a knowledge base for an ecosystem management plan. Douglas, WY.

Craig, T.H., J.W. Connelly, E.H. Craig, and T.L. Parker. 1990. Lead concentrations in golden and bald eagles. Wilson Bull. 102: 130-133.

Evers, D.C., N.M. Burgess, L. Champoux, B. Hoskins, A. Major, W. Goodale, R. Taylor, R. Poppenga, and T. Daigle. 2005. Patterns and interpretation on mercury exposure in freshwater avian communities in northeastern North America. Ecotox. 14: 193-221.

Fernandez, F.J. and D. Hilligoss. 1982. Improved graphite furnace method for determination of lead in blood using matrix modification and the L'vov platform. Atom. Spec. 3: 130-131.

Franson, C.J. 1986. Immunosuppressive effects of lead. In: *Lead Poisoning in Wild Waterfowl: A Workshop*, J.S. Feierabend and A.B. Russell, eds. National Wildlife Federation. Washington D.C. Pp. 106-109.

Franson, J.C. 1996. Interpretation of tissue lead residues in birds other than waterfowl. In: W.N. Beyer, G.H. Heinz, and A.W. Redmon-Norwood, eds. *Environmental Contaminants in Wildlife*: *Interpreting Tissue Concentrations*. CRC Press, Inc. Boca Raton, Florida. pp. 265-279.

Franson, J.C., W.L. Hohman, J.L. Moore, and M.R. Smith. 1996. Efficacy of protoporphyrin as a predictive marker for lead exposure in canvasback ducks: Effect of sample storage time. Environ. Monit. Assess. 43: 181-188.

Franson, J.C., L. Sileo, O.H. Pattee, and J.F. Moore. 1983. Effects of chronic dietary lead in American kestrels (*Falco sparverius*). J. Wildl. Diseas. 19: 110-113.

Golden, N.H., B.A. Rattner, J.B. Cohen, D.J. Hoffman, E. Russek-Cohen, and M.A. Ottinger. 2003. Lead accumulation in feathers of nestling black-crowned night herons (*Nycticorax nycticorax*) experimentally treated in the field. Environ. Toxicol. Chem. 22: 1515-1524.

Henny C.J., L.J. Blus, D.J. Hoffman, L. Sileo, D.J. Audet, and M.R. Snyder. 2000. Field evaluation of lead effects on Canada geese and mallards in the Coeur d’Alene River Basin, Idaho. Arch. Environ. Contam. Toxicol. 39: 97-112.

Hoffman, D.J., J.C. Franson, O.H. Pattee, C.M.Bunck, and A. Allen. 1985a. Survival, growth, and accumulation of ingested lead in nestling American kestrels (*Falco sparverius*). Arch. Environ. Contam. Toxicol. 14: 89-94.

Hoffman, D.J., J.C. Franson, O.H. Pattee, C.M.Bunck, and H.C. Murray. 1985b. Biochemical and hematological effects of lead ingestion in nestling American kestrels (*Falco sparverius*). Comp. Biochem. Physiol. 80C: 431-439.

Jacobson, E., J.W. Carpenter, and M. Novilla. 1977. Suspected lead toxicosis in a bald eagle. J. Am. Vet. Med. Assoc. 171: 952-954.

Leonzio, C. and M.C. Fossi. 1994. Nondestructive biomarker strategy: Perspectives and applications. In: M.C. Fossi and C. Leonzio, eds. *Nondestructive Biomarkers in Vertebrates*. CRC Press, Inc. Boca Raton, Florida. pp. 297-312.

Locke, L.N., G.E. Bagley, D.N. Frickie, and L.T. Young. 1969. Lead poisoning and aspergillosis in an Andean condor. J. Am. Vet. Med. Assoc. 155: 1052-1056.

Mayer, F.L., D.J. Versteeg, M.J. McKee, L.C. Folmar, R.L. Graney, D.C. McCume, and B.A. Rattner. 1992. Physiological and nonspecific biomarkers. In: R.J. Huggett, R.A. Kimerle, P.M. Mehrl, Jr., and H.L. Bergman, eds. *Biomarkers: Biochemical, Physiological, and Histological Markers of Anthropogenic Stress*. Lewis Publishers. Chelsea, Michigan. pp.5-85.

Miller, M.J.R., M.E. Wayland, E.H. Dzus, and G.R. Bortolotti. 2000. Availability and ingestion of lead shotshell pellets by migrant bald eagles in Saskatchewan. J. Raptor Res. 34: 167-174.

Pain, D.J. 1995. Lead in the environment. In: D.J. Hoffman, B.A. Rattner, G.A. Burton, Jr., and J. Cairns, Jr., eds. *Handbook of Ecotoxicology*. Lewis Publishers, Boca Raton, Florida. pp.356-391.

Pain, D.J. 1996. Lead in waterfowl. In: W.N. Beyer, G.H. Heinz, and A.W. Redmon-Norwood, eds. *Environmental Contaminants in Wildlife*: *Interpreting Tissue Concentrations*. CRC Press, Inc. Boca Raton, Florida. pp. 265-279.

Pattee, O.H. 1984. Eggshell thickness and reproduction in American kestrels exposed to chronic dietary lead. Arch. Environ. Contam. Toxicol. 13: 29-34.

Pattee, O.H., S.N. Wiemeyer, B.M. Mulhern, L. Sileo, and J.W. Carpenter. 1981. Experimental lead-shot poisoning in bald eagles. J Wildl. Manage. 45: 1981.

Platt, J.B. 1976. Bald eagles wintering in the Utah desert. Am. Birds. 30: 783-788.

Rawson, R.E., G.D. DelGiudice, H.E. Dziuk, and L.D. Mech. 1992. Energy metabolism and hematology of white-tailed deer fawns. J. Wildl. Dis. 28: 91-94.

Redig, P.T., C.M. Stowe, D.M. Barnes, and T.D. Arent. 1980. Lead toxicosis in raptors. J. Am. Vet. Med. Assoc. 177: 941-943.

Sari M., S. de Pee, E. Martini, S. Herman, W. Sugiatmi, M. Bloem, and R. Yip. 2001. Estimating the prevalence of anemia: A comparison of three methods. Bull. World Health Org. 79: 506-511.

United States Fish and Wildlife Service. 2000. Fish and Wildlife News. September/October 2000. Washington D.C. Pg. 6.

United States Fish and Wildlife Service. 1996. Standard Operating Procedures for Environmental Contaminants Operations. Volume 1. Department of Interior, Washington D.C.

United States Fish and Wildlife Service. 1986. Use of lead shot for hunting migratory birds in the United States. Final supplemental environmental impact statement. Department of Interior, Washington D.C.

United States Forest Service and United States Bureau of Land Management. 1992. Oil and gas leasing on the Thunder Basin National Grassland. Final Environmental Impact Statement. Douglas Ranger District. Various pages.

Wobeser, G.A. 1981. *Diseases of Wild Waterfowl*. Plenum Press, New York. 300 pp.

Wyoming Game and Fish Department. 1995. Endangered and non-game bird and mammal investigations. 1995 Annual Completion Report. Cheyenne, Wyoming.

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**General Technical
Report RM-GTR-298**

Conserving Biodiversity on Native Rangelands: Symposium Proceedings

August 17, 1995

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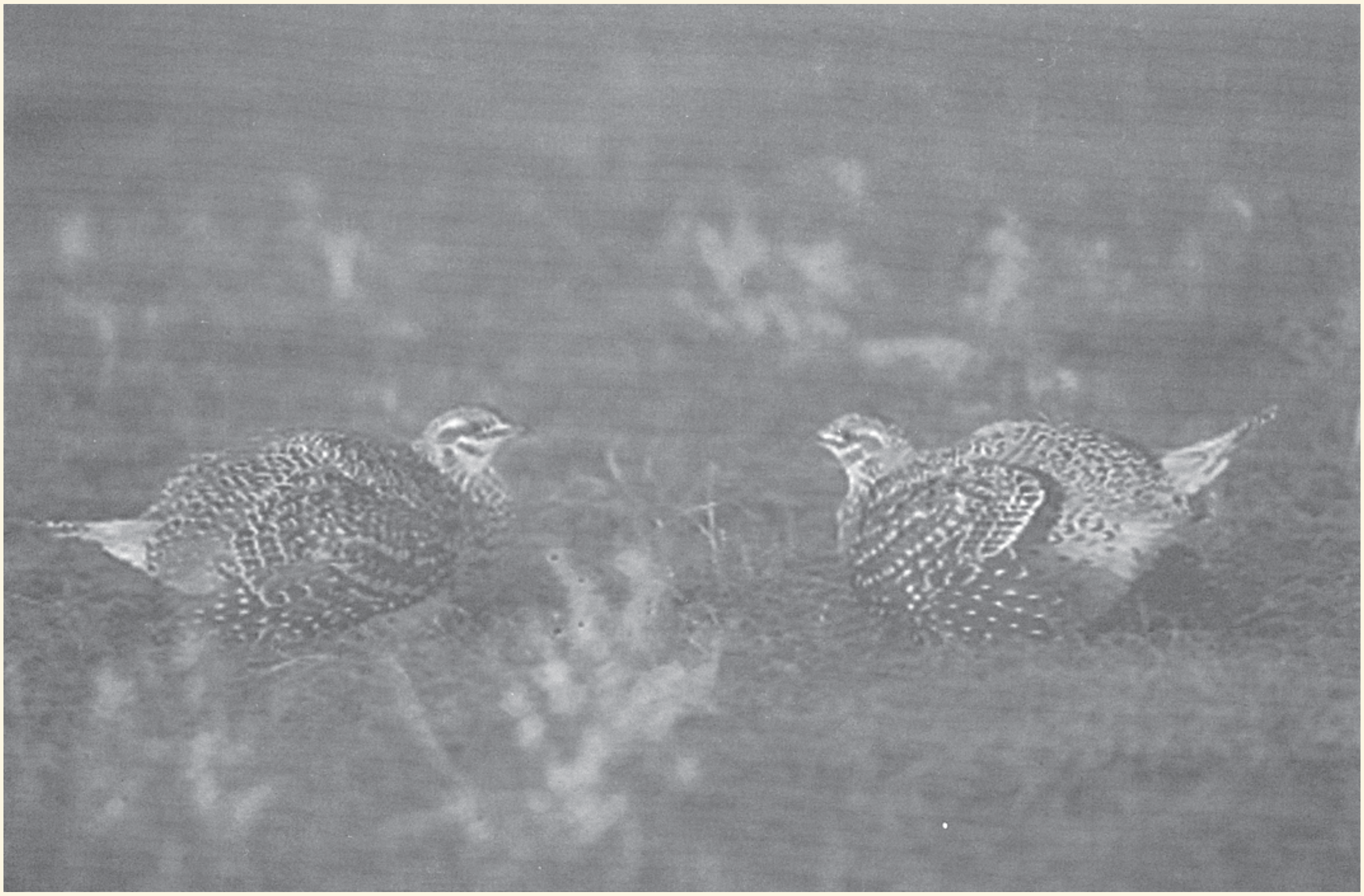

Uresk, Daniel W.; Greg L. Schenbeck; James T. O'Rourke, tech coords. 1996. Conserving biodiversity on native rangelands: symposium proceedings; August 17, 1995; Fort Robinson State Park, Nebraska. General Technical Report RM-GTR-298. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 38 p.

Abstract: These proceedings are the result of a symposium, "Conserving biodiversity on native rangelands" held on August 17, 1995 in Fort Robinson State Park, NE. The purpose of this symposium was to provide a forum to discuss how elements of rangeland biodiversity are being conserved today. We asked, "How resilient and sustainable are rangeland systems to the increasing demands of a growing human population and to extended periods of drought?" Key programs and issues, identified by a program committee, were addressed by researchers and managers. Their papers provide research results, management findings, and describe management programs currently used to conserve rangeland biodiversity.

Keywords: biodiversity, rangeland, sustainability, drought, conservation

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Conserving Biodiversity on Native Rangelands: Symposium Proceedings

August 17, 1995

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Nebraska Chapter of The Wildlife Society

Contents

Introduction

Rangelands embody biological diversity of profound ecological and social significance, yet it is the biological diversity of forests and wetlands that has been the focus of research by scientists and concern by the public. Recently, a broad array of people, from ecologists and biologists to ranchers and recreationists, have begun to realize the importance of rangeland conservation and biological diversity. Although these groups may not always share a common vision of rangelands, they share a common interest in the land that will foster a better understanding and appreciation of the value of diverse and healthy rangelands.

Ranchers have long practiced conservation of rangeland biological diversity. Most recognize the importance of both warm and cool season grasses to round out their forage programs, and many have noticed that in some years one grass will do poorly while another will thrive, thus balancing the production. Ranchers depend on native grasses coming back on their own after drought or a bad grasshopper year; some species will return quicker than others. Looking toward the future, ranchers manage their grass for a diverse rangeland community, not a monotypic one. This is conservation of rangeland biological diversity at the grass roots level.

Together, scientists and rangeland managers are traveling to new levels of conservation of rangeland biodiversity, but the journey has some formidable challenges. Herbivory, fire, drought, and other natural events and processes historically shaped rangeland biodiversity and ecological processes long before human action. However, human influence on the range has complicated and interrupted many naturally occurring mechanisms. The use and control of fire has altered its frequency and intensity. The pattern, frequency, and intensity of herbivory by large animals has been modified by the conversion from free-ranging bison and other large ungulates to confined domestic livestock and a proliferation of livestock water developments. Cultivation has fragmented and isolated rangelands and often natural processes no longer function. An insidious challenge to rangeland biodiversity is the invasion of exotic plants into native range often at the expense of native biota.

The purpose of this symposium was to provide a forum to discuss how elements of rangeland biodiversity are being conserved today. We asked, "How resilient and sustainable are rangeland systems to the increasing demands of a growing human population and to extended periods of drought?" One way to begin answering this question is to look at our successes and failures in conserving all parts of rangeland systems. Key programs and issues, identified by a program committee, were addressed by researchers and managers. Their papers, which have received statistical and peer review, are presented here and provide research results, management findings, and describe management programs currently used to conserve rangeland biodiversity. The paper "Gap Analysis in the Great Plains: A Large-Scale Geographic Strategy for Conservation of Biodiversity" by Dennis Jelinski, Michael Jennings, and James Merchant was withdrawn by the authors before publication of this workshop proceedings.

This symposium was held concurrently with the Annual Meeting of the Central Mountains and Plains Section of The Wildlife Society. We thank the organizers of that event for suggesting this symposium. Thanks are also extended for the well-attended field trip to review northern swift fox management in southwestern South Dakota that concluded the workshop.

A Neotropical Migratory Bird Prioritization for National Forests and Grasslands

Dick Roth[1] and Richard Peterson[2]

Abstract.-The Rocky Mountain Region of the USDA Forest Service provides nesting habitat for 146 species of neotropical migratory birds. Interactive, prioritization databases were developed for each National Forest and National Grassland in the Region to assist land managers in making informed decisions about resource allocations. The data was processed using Paradox software. This paper summarizes the uses and application of the database for the Oglala and Ft. Pierre National Grasslands.

METHODS

We used data provided by Colorado Bird Observatory and ranked according to the Partners-In-Flight (PIF) ranking scheme for initial prioritization of neotropical migratory birds (NTMBs). The approach ranks species by their relative susceptibility to extinction (Carter and Barker 1993, Hunter et al. 1993). There are many factors that contribute to extinction probability. The PIF prioritization scheme uses seven criteria as the most important in gauging a species susceptibility to extirpation or extinction: 1) importance of area of consideration (IA), (percentage of a species range that is within a state or geographic area under consideration); 2) global abundance (GA); 3) the degree of threat to the species' persistence on the breeding ground (TB); 4) the degree of threat to species' persistence on the wintering ground (TW); 5) breeding distribution (BD); 6) extent of wintering distribution (WD); 7) population trend in area of consideration (PT); based upon U.S. Fish and Wildlife Service Breeding Bird Survey (BBS) data. Each of the seven criteria is weighted equally. An individual species is assigned a score in each of the seven categories ranging from one (low concern) to five (high concern). Each species is ranked according to the average of the seven scores. The importance of area score (IA) was modified for our use to include a rank based upon the percentage of the area under consideration which meets breeding habitat requirements for a given species.

Uncertainty values are assigned to each species in conjunction withvalues assigned for threats to breeding (TBU) and wintering (TWU), and population trend (PTU). These uncertainty values reflect the extent of the available information for each of the associated criteria. They indicate the extent and location of gaps in our knowledge of neotropical migrant biology. These values help us differentiate between species withdefinite management concerns and those requiring additional monitoring or research in order to more clearly reflect their status.

Several criteria were modified for the Oglala and Ft. Pierre National Grasslands. Population trend (PT) and Population trend uncertainty scores were determined from USFWS Breeding Bird Survey (BBS) for the lo-year and 26-year scores. Data from physiorgraphic region 39 (Missouri Plateau-Unglaciated) were used for both grasslands. Other population trend data more specific to the area under considerationcanbe used for these criteria if available. Threats to breeding habitat (TB) and Threats to breeding habitat uncertainty (TBU) criteria provided by PIF were used (Carter and Barker 1993). Additionally, known local threats were also considered such as reduction of prairie dog towns as a threat to burrowing owl habitat. In this case, a TB score of 5 was used because loss of prairie dog towns would result in eliminationof burrowing owl habitat (Peterson 1994).

Several methods have been developed to determine priorities for community based conservation (Millsap et al. 1990, Master 1991, Reed 1992). The technique developed by Partners in Flight is essentially one that ranks individual species first, and secondarily ranks habitats based on individual species scores grouped by habitat preference. This ranking can then be used to develop and justify community based conservation programs. The

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tion of breeding occurrence and habitat preference of neotropical migratory landbirds on the Oglala and Ft. Pierre Grasslands was made using local expertise.

The habitat types and conditions developed for the Grasslands and assigned to each species have three levels:

1) Appropriate habitat contains six major breeding bird habitat types. They include trees/woodlands, shrubs/shrublands, grass/grasslands, edge-tree/grass-shrub/grass, wetlands and special topographic structure.
2) Suitable habitat, in general, additional conditions are needed for appropriate habitat to be suitable breeding habitat for a given species. For grasslands, additional conditions could be related to a given height and density of grasses or forbs. For trees/woodland habitat, additional conditions could include deciduous trees, cavities or a multi-layered canopy.
3) Special conditions includes topographic structures such as cliffs and cutbanks, but also includes features such as riparian areas and prairie dog towns.

These habitat categories enable development of habitat ranking based on a species' use of a wide variety of habitat types and variables.

Coding used for habitats and special features is as follows:

Habitats T-(t)rees/woodlands, coni(f)erous, (d)ediduous, (o)ld growth, m(u)ltilayer canopy, and
(c)avities.
E-(e)dge, tree-grass/shrub-grass.
S-(s)hrubs, (b)ig sagebrush, (2) thorny shrubs-esp. plum,
G-(g)rass/grasslands-open areas-esp. s(h)ort and/or sparse, t(a)ll and/or de(n)se, mi(x)ed/mid.
W-(w)etlands/(w)ater-(1)riparian, (m)arsh/tall emergent, (3) wet meadow-tall grass/short emergent.
Specials s(P)ecial-top/structure-(4)cliffs/caves/ledges and cutbanks, (5)buildings/bridges/chimneys and bird houses, lands/bare shores.
s(p)ecial-other-(7)prairie dog towns, (i.e. burrows/bare ground/short grass and associated prey), forest fire locations-(B)urned areas, esp. large with tall snags, (9) cropland-esp alfalfa, (O)old crow/magpie nests.

The mix of numbers and letters used in the coding may appear to be confusing; however, familiarization with the application of those codes as displayed in the habitat columns of the accompanying tables reveals that they provide a logical fit.

RESULTS

The Oglala and Ft. Pierre National Grasslands support 79 and 68 species of neotropical migratory landbirds which regularly nest there, or a combined total of 84 regular nesters. These are listed in Appendix 1 and 2 along with all associated prioritization scores for the seven criteria and some of the associated uncertainty scores. Species with R10 or R26 ranks of 3.00 or greater should be given high priority for management considerations (Thompson et al. 1993). Analysis of the data reveals that 18 of the 84 species have a R10 or R26 rank of 3.00 or greater (Appendix 1 and 2). The R10 and R26rank scores along with importance of area, threats to breeding and breeding distribution scores help to provide a framework for setting management priorities. As an illustration, the chestnut-collard longspur has high and R26 rank scores but has an importance of area (IA) score of only 3.00.

Consequently, other species with higher IA scores should be given higher management priority. The two top ranked species on both grasslands (burrowing owl and ferruginous hawk) have a preference for short-grass prairie and prairie dog towns. Other species on these two grassland have a preference for tall and mixed-grass prairie. Consequently, management of the National Grassland units for a diversity of heights and would provide habitat for both species.

The database contains scores for each criterion, for each species, for each unit where they are likely to occur. It is important that the data for each unit be analyzed separately for more specific insights into the top priority species and habitat for each unit. For example, what is the importance of the habitat on the unit being analyzed for a given species. What are the threats to that habitat? What is the status and trend of that habitat?

This prioritization system reveals that the highest ranked habitat on the Oglala National Grassland is big sagebrush and that is based on one species (table 1). The next highest ranked habitat is short and mixed-grass prairie and prairie dog towns respectively. These habitats support six and four high priority (= > 3) species respectively. Edge habitat and riparian habitat are both important because of the diversity of species that they support. These values are based upon the relative susceptibility to extinction of species found in each habitat. Information on species as presented in table 2 should also be considered along with the habitat information when weighing the consequences of management actions.

A total of 12 species from the Oglala National Grassland have a R26 Rank of 3.00 or greater. Brewer's Sparrow is the species in big sagebrush habitat which causes the high habitat rank in table 1. The rank of 1 for importance of area score (IA) indicates that only a small portion of the Oglala National Grassland provides suitable breeding habitat for Brewer's Sparrows. The two top-ranked species use prairie dog towns and the top five species also short to mixed grass prairie habitats.Therefore, the highest priority habitats for NTMBs on the Oglala National Grassland should be those that support these species.

Table 1. Habitat association scores for the Oglala National Grassland based on R26 species ranks.

Habitat	≤3	<3 to 2	<1 .99	# Species	Average score	Total score
Short/Mix Grass	6	1	1	8	3.08	24.71
Prairie Dog Towns	4	2	1	7	2.94	20.57
Mix/tall Grass	2	7		9	2.81	29.00
Trees Deciduous	2	8	2	12	2.48	29.71
Shrub Big Sage	1			1	3.14	3.14
Shrub Dense		5		5	2.60	13.00
Edge	1	15	7	23	2.32	53.41
Water/marsh		7	4	11	2.18	24.00
Riparian	2	15	5	22	2.36	51.99

Table 2. Species on the Oglala National Grassland with 10R10 or R=≥3.00.

Species	Hab	IA	AB	TB	BD	R10	R26
Burrowing Owl	Gh7	5	4	5	3	3.57	3.86
Long-billed Curlew	Gxh7	5	3	3	4	3.86	3.71
Chestnut-collared Longspur	Gxh	3	3	3	4	3.29	3.57
Lark Bunting	Gxhs	5	2	3	4	3.29	3.43
Ferruginous Hawk	Gxht7	3	4	4	3	3.29	3.29
Black-billed Cuckoo	Tds12	2	3	4	3	3.29	3.14
Bobolink*	Ga39	1	2	4	3	3.14	3.14
Brewer's Sparrow	Sb	1	2	4	3	3.00	3.14
Loggerhead Shrike	Es2	3	3	4	2	3.00	3.14
Dickcissel*	Ga9	1	2	4	3	2.86	3.00
Great Crested Flycatcher	Tdcl	1	2	4	3	3.00	3.00
Prairie Falcon	Gxh47	4	3	3	3	3.14	3.00

** Species found in the area but not confirmed nester on National Grassland.*

Similar analysis of the data for the Ft Pierre National Grassland reveals somewhat different results (table 3). Ft Pierre is in a higher precipitation area and has taller grasses and more deciduous trees than the Oglala National Grassland. Bird species diversity is greater across habitat types than on the Oglala National Grassland and mixed/tall grass habitat higher priority. The burrowing owl is the highest ranked species on both units (table 4). Dickcissel , bobolink, grasshopper sparrow, northern harrier and upland sandpiper had higher prioritization scores on the Ft. Pierre National Grassland. Management of prairie dog towns and short grass habitat should have some priority on Ft. Pierre, but management for mixed to tall grass habitat is of higher priority based on this analysis.

Table 3. Habitat association scores for the Ft. Pierre National Grassland based on R26 species ranks.

Habitat	≥3	>3 to 2	>1.99	# Species	Average score	Total score
Short/Mix Grass	5	1	1	7	3.06	21.43
Prairie Dog Towns	3	2	1	6	2.81	16.86
Mix/Tall Grass	5	5		10	3.13	31.29
Trees Deciduous	2	9	2	13	2.50	32.58
Shrub Dense	1	5		6	2.26	13.57
Edge	1	9	7	17	1.98	33.70
Water/marsh	1	8	5	14	2.01	28.13
Riparian	3	14	5	22	2.39	52.58

Table 4. Species on Ft. Pierre National Grassland with RIO **or** R26 **scores ≥** 3.00.

Species	Hab	IA	TB	BD	AB	R10	R26
Burrowing Owl	Gh7	4	5	3	5	3.57	3.86
Baird's Sparrow*(Historic)	Gx3	4	5	5	0	3.86	3.71
Chestnut-collared Longspur	Gxh	3	3	4	3	3.29	3.57
Dickcissel	Ga9	2	3	3	5	3.29	3.43
Ferruginous Hawk	Gxht7	4	4	3	4	3.43	3.43
Lark Bunting	Gxhs	2	3	4	5	3.29	3.43
Bobolink	Ga39	2	3	3	3	3.29	3.29
Long-billed Curlew*	Gxh7	3	4	4	1	3.43	3.29
Bell's Vireo*	Sn12	3	4	3	1	3.14	3.14
Black-billed Cuckoo	Tdsl2	3	4	3	2	3.29	3.14
Grasshopper Sparrow	Gxa	2	2	2	5	2.57	3.00
Great Chrested Flycatcher*	Tdcl	2	4	3	1	3.00	3.00
Loggerhead Shrike	Es2	3	4	2	2	2.86	3.00
Northern Harrier	Gasm	3	3	1	5	3.00	3.00
Sprague's Pipit*(historic)	Gxa	3	5	4	0	3.00	3.00
Upland Sandpiper	Gx	3	2	3	5	3.14	3.00

Species found in the area but not confirmed nester on National Grassland.

CONCLUSIONS

The PIF species ranking system is a helpful tool in establishing priorities for Neotropical Migratory Bird species and habitat based management efforts for those species. It should not replace human judgment or additional information which might be important in setting resource priorities. Refinement of the PIF data as was done on the Oglala and Ft. Pierre National Grasslands with local expertise increases the utility value of the system. Only a few analysis examples were given here. However, an endless variety of queries can be used to tease additional information from the data.

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LITERATURE CITED

Carter, Michael F. and Keith Barker., 1993. An Interactive Database for Setting Conservation Priorities for Western Neotropical Migrants. Pages 120-144 *in*. Finch and Stangel, eds. Status and Management of NTMB. USDA. Forest Service, General Technical Report RM 229.

Hunter, William C., David N. Pashley, and Ronald E.F. Escano. 1993. Neotropical Migratory Landbird Species and Their Habitats of Special Concern Within the Southeast Region. Pages 159-171 *in*. Finch and Stangel, eds. Status and Management of NTMB. USDA. Forest Service, General Technical Report. RM 229.

Master, L., 1991 Assessing threats and setting priorities for conservation. Cons. Biol. 5.559-563.

Millsap, B.A., J.A. Gore, D.E. Runde, and S.I. Cerulean. 1990. Setting priorities for the conservation of fish and wildlife species in Florida. Wildl. Monogr. 111.

Peterson, Richard A. 1994. Nebraska National Forest Neotropical Migrant Landbird Conservation Priorities. Unpubl. Rep. USDA Forest Service, Chadron. NE. 38pp.

Reed, Michael., 1992. A system for ranking conservation priorities for neotropical migrant birds based on relative susceptibility to extinction. Pp. 524-536. in Ecology and conservation of neotropical migrant landbirds. (J.M. Hagan III and D.W. Johnston, eds.). Washington and London, Smithsonian Institute.

Thompson, Frank R., Stephen J. Lewis, Janet Green and David Ewert. 1993. Status of NTM Landbirds in the Midwest: Identifying Species of Management concern. Pp. 145-153. in (Finch and Stangel (ed.). Status and Management of NTMB. USDA Forest Service, General Technical Report RM 229.

Appendix 1. **Prioritization scores for the Neotropical Migratory Landbirds of the Oglala National Grasslands.**

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
American Goldfinch	Tdes1	1.00	2.00	3.00	1.00	1.00	2.00	3.00	3.00	2.00	3.00	1.43	1.57
American Kestrel	Ec8	1.00	1.00	2.00	2.00	1.00	4.00	1.00	1.00	2.00	3.00	1.71	1.57
American Robin	Ethw	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00	4.00	3.00	1.57	1.29
Barn Swallow	Pgw5	1.00	1.00	1.00	2.00	1.00	2.00	1.00	1.00	5.00	1.00	1.86	1.29
Belted Kingfisher	W4	2.00	4.00	2.00	2.00	1.00	1.00	4.00	3.00	3.00	4.00	2.00	2.14
Black-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	3.00	2.00	3.00	3.00	4.00	3.00	3.29	3.14
Black-headed Grosbeak	Tdsl	2.00	3.00	4.00	2.00	3.00	2.00	2.00	3.00	2.00	2.00	2.57	2.57
Blue Grosbeak	Sn2	3.00	3.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.43	2.57
Bobolink	Ga39	2.00	4.00	2.00	3.00	3.00	1.00	5.00	2.00	5.00	2.00	3.14	3.14
Brewer's Blackbird	Es29	2.00	3.00	5.00	2.00	3.00	1.00	3.00	3.00	3.00	3.00	2.29	2.29
Brewer's Sparrow	Sb	2.00	4.00	3.00	4.00	3.00	1.00	5.00	1.00	4.00	3.00	3.00	3.14
Brown-headed Cowbird	Egsm	1.00	1.00	1.00	1.00	1.00	5.00	1.00	1.00	1.00	1.00	1.71	1.71
Burrowing Owl	Gh7	4.00	5.00	2.00	3.00	3.00	5.00	4.00	3.00	2.00	3.00	3.57	3.86
Cedar Waxwing	Ts	2.00	2.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.00	2.14
Chestnut-collared Longspur	Gxh	3.00	3.00	4.00	4.00	4.00	3.00	4.00	3.00	2.00	3.00	3.29	3.57
Chipping Sparrow	Efs	1.00	3.00	4.00	2.00	1.00	3.00	4.00	3.00	4.00	3.00	2.29	2.29
Cliff Swallow	Pw45	2.00	2.00	4.00	2.00	1.00	1.00	3.00	3.00	3.00	3.00	2.00	2.00
Common Nighthawk	Eh	2.00	2.00	4.00	2.00	1.00	5.00	3.00	3.00	4.00	3.00	2.43	2.29
Common Poorwill	Ef4	3.00	2.00	4.00	3.00	3.00	2.00	3.00	4.00	3.00	4.00	2.71	2.71
Common Yellowthroat	Wmsl	1.00	3.00	2.00	2.00	1.00	2.00	4.00	3.00	5.00	2.00	2.29	2.14
Cooper's Hawk	To1	3.00	3.00	3.00	3.00	1.00	1.00	3.00	4.00	3.00	5.00	2.29	2.29
Dickcissel	Ga9	2.00	4.00	3.00	2.00	3.00	1.00	5.00	1.00	4.00	3.00	2.86	3.00
Eastern Bluebird	Ec85	2.00	3.00	2.00	3.00	3.00	1.00	3.00	4.00	3.00	4.00	2.43	2.43
Eastern Kingbird	E	1.00	1.00	2.00	3.00	2.00	3.00	2.00	3.00	1.00	1.00	2.00	2.14
Eastern Phoebe	Td15	2.00	4.00	4.00	3.00	3.00	1.00	3.00	4.00	3.00	5.00	2.57	2.57
Ferruginous Hawk	Gxht7	4.00	4.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.29	3.29
Golden Eagle	Et47	3.00	2.00	2.00	2.00	2.00	5.00	4.00	3.00	2.00	3.00	2.57	2.86
Grasshopper Sparrow	Gxa	2.00	2.00	3.00	2.00	2.00	4.00	5.00	1.00	2.00	3.00	2.43	2.86
Gray Catbird	Sn12	2.00	4.00	2.00	2.00	2.00	2.00	4.00	2.00	2.00	3.00	2.43	2.71
Great Crested Flycatcher	Tdcl	2.00	4.00	3.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	3.00	3.00
Horned Lark	Gh7	1.00	1.00	1.00	1.00	1.00	5.00	2.00	2.00	2.00	3.00	1.71	1.71
House Wren	Tc15	1.00	2.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	2.00	1.29	1.29
Indigo Bunting	Tdsl	1.00	3.00	3.00	2.00	3.00	1.00	3.00	4.00	3.00	4.00	2.29	2.29
Killdeer	Gh67	1.00	2.00	2.00	1.00	1.00	5.00	4.00	1.00	5.00	1.00	2.29	2.14
Lark Bunting	Gxhs	2.00	3.00	3.00	3.00	4.00	5.00	4.00	2.00	3.00	3.00	3.29	3.43
Lark Sparrow	E	3.00	2.00	3.00	2.00	2.00	3.00	3.00	3.00	1.00	2.00	2.29	2.57
Lazuli Bunting	Tsl	2.00	3.00	4.00	2.00	3.00	2.00	4.00	3.00	2.00	3.00	2.57	2.86
Loggerhead Shrike	Es2	3.00	4.00	4.00	4.00	2.00	3.00	3.00	3.00	2.00	2.00	3.00	3.14
Long-billed Curlew	Gxh7	3.00	3.00	4.00	3.00	4.00	5.00	4.00	3.00	5.00	1.00	3.86	3.71
Long-eared Owl	Efo0	3.00	3.00	3.00	3.00	1.00	1.00	3.00	5.00	3.00	5.00	2.14	2.14

Appendix 1 (Continued).

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
Marsh Wren	Wm	2.00	4.00	2.00	4.00	3.00	2.00	3.00	4.00	3.00	4.00	2.71	2.71
Merlin	Ef0	4.00	4.00	4.00	3.00	2.00	2.00	3.00	4.00	3.00	4.00	2.86	2.86
Mountain Bluebird	Ec85	2.00	3.00	3.00	3.00	3.00	2.00	4.00	2.00	3.00	3.00	2.57	2.71
Mourning Dove	Ew	1.00	1.00	1.00	1.00	1.00	4.00	1.00	1.00	3.00	3.00	1.71	1.43
N. Rough-winged Swallow	Pw4	3.00	3.00	3.00	2.00	1.00	2.00	4.00	3.00	3.00	3.00	2.43	2.57
Northern Flicker	Ec8	1.00	2.00	1.00	1.00	1.00	2.00	4.00	2.00	3.00	3.00	1.57	1.71
Northern Harrier	Gasm	3.00	4.00	3.00	4.00	1.00	3.00	4.00	3.00	4.00	3.00	2.86	2.86
Northern Mockingbird	Eds12	1.00	2.00	2.00	1.00	2.00	1.00	3.00	4.00	3.00	4.00	1.71	1.71
Northern Oriole	Tdsl	2.00	3.00	3.00	2.00	2.00	2.00	3.00	3.00	3.00	3.00	2.43	2.43
Orchard Oriole	Tdsl	3.00	3.00	3.00	2.00	3.00	2.00	2.00	2.00	4.00	3.00	2.86	2.57
Oven bird	Tu	2.00	4.00	4.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	2.86	2.86
Pine Siskin	Tfe	1.00	2.00	3.00	1.00	2.00	2.00	3.00	4.00	3.00	4.00	1.71	1.71
Prairie Falcon	Gxh47	3.00	3.00	3.00	3.00	3.00	4.00	3.00	3.00	4.00	3.00	3.14	3.00
Red-eyed Vireo	Tdul	1.00	4.00	4.00	2.00	2.00	1.00	3.00	3.00	3.00	4.00	2.29	2.29
Red-tailed Hawk	Etg	1.00	2.00	2.00	2.00	1.00	5.00	3.00	3.00	3.00	3.00	2.14	2.14
Red-winged Blackbird	Wms1	1.00	2.00	1.00	1.00	1.00	2.00	4.00	2.00	4.00	3.00	1.71	1.71
Rock Wren	P4	3.00	2.00	2.00	2.00	3.00	3.00	4.00	2.00	4.00	3.00	2.71	2.71
Rufous-sided Towhee	Sn	1.00	3.00	4.00	2.00	2.00	2.00	4.00	3.00	4.00	3.00	2.29	2.29
Say’s Phoebe	G45	3.00	2.00	3.00	3.00	2.00	3.00	3.00	3.00	3.00	3.00	2.71	2.71
Sharp-shinned Hawk	Tfo	3.00	3.00	2.00	3.00	1.00	1.00	3.00	4.00	3.00	4.00	2.14	2.14
Short-eared Owl	Gasm	3.00	4.00	4.00	4.00	1.00	2.00	2.00	3.00	4.00	3.00	2.71	2.43
Swainson’s Hawk	Gxt9	3.00	2.00	2.00	3.00	2.00	5.00	2.00	1.00	2.00	3.00	2.86	2.86
Tree Swallow	Ec15	2.00	4.00	3.00	3.00	1.00	1.00	2.00	3.00	3.00	3.00	2.29	2.14
Turkey Vulture	E4	1.00	2.00	4.00	2.00	1.00	4.00	2.00	2.00	4.00	3.00	2.14	1.86
Upland Sandpiper	Gx	3.00	2.00	3.00	3.00	3.00	4.00	2.00	3.00	3.00	3.00	3.00	2.86
Vesper Sparrow	Gxs	3.00	3.00	4.00	2.00	2.00	2.00	4.00	3.00	4.00	3.00	2.57	2.57
Violet-green Swallow	Efc4	2.00	3.00	3.00	2.00	3.00	2.00	3.00	4.00	3.00	4.00	2.57	2.57
Warbling Vireo	Td1	2.00	3.00	4.00	2.00	2.00	2.00	5.00	1.00	4.00	3.00	2.57	2.71
Western Kingbird	E	1.00	1.00	2.00	2.00	3.00	3.00	1.00	1.00	1.00	2.00	2.14	2.14
Western Meadowlark	Gx7	1.00	2.00	2.00	3.00	2.00	5.00	3.00	3.00	3.00	3.00	2.43	2.43
Western Tanager	Tf	2.00	3.00	4.00	2.00	3.00	2.00	3.00	4.00	3.00	4.00	2.57	2.57
Western Wood-Pewee	T	2.00	3.00	4.00	3.00	2.00	2.00	2.00	2.00	1.00	1.00	2.43	2.57
White-throated Swift	P4	3.00	2.00	3.00	2.00	3.00	1.00	3.00	4.00	3.00	4.00	2.43	2.43
Willow Flycatcher	**Sn12**	3.00	4.00	3.00	3.00	3.00	1.00	3.00	5.00	4.00	3.00	3.00	2.86
Yellow Warbler	Tds1	1.00	4.00	3.00	2.00	1.00	2.00	2.00	3.00	2.00	3.00	1.86	1.86
Yellow-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	2.00	2.00	2.00	3.00	3.00	4.00	2.86	2.71
Yellow-breasted Chat	Sn12	2.00	3.00	3.00	3.00	2.00	2.00	3.00	3.00	1.00	1.00	2.29	2.57
Yellow-headed Blackbird	Wm	3.00	4.00	2.00	3.00	3.00	2.00	2.00	3.00	4.00	3.00	3.14	2.86
Yellow-rumped Warbler	Tf	1.00	2.00	2.00	1.00	1.00	2.00		4.00	3.00	4.00	1.71	1.29

Appendix 2. Prioritization scores for the Neotropical Migratory Landbirds of the Ft. Pierre National Grasslands.

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
American Goldfinch	Tdes1	1.00	2.00	3.00	1.00	1.00	2.00	3.00	3.00	2.00	3.00	1.43	1.57
American Kestrel	Ec8	1.00	2.00	2.00	2.00	1.00	4.00	1.00	1.00	2.00	3.00	1.86	1.71
American Robin	Ethw	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00	4.00	3.00	1.57	1.29
Baird's Sparrow(historic)	Gx3	4.00	5.00	4.00	4.00	5.00	0.00	4.00	3.00	5.00	2.00	3.86	3.71
Bank Swallow	Pw4	3.00	3.00	4.00	2.00	1.00	1.00	2.00	3.00	2.00	2.00	2.14	2.14
Barn Swallow	Pgw5	1.00	1.00	1.00	2.00	1.00	2.00	1.00	1.00	5.00	1.00	1.86	1.29
Bell's Vireo	Sn12	3.00	4.00	3.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	3.14	3.14
Belted Kingfisher	w4	2.00	4.00	2.00	2.00	1.00	1.00	4.00	3.00	3.00	4.00	2.00	2.14
Black-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	3.00	2.00	3.00	3.00	4.00	3.00	3.29	3.14
Black-headed Grosbeak	Tds1	2.00	3.00	4.00	2.00	3.00	1.00	2.00	3.00	2.00	2.00	2.43	2.43
Blue Grosbeak	Sn2	3.00	3.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.43	2.57
Bobolink	Ga39	2.00	3.00	2.00	3.00	3.00	3.00	5.00	2.00	5.00	2.00	3.29	3.29
Brown-headed Cowbird	Egsm	1.00	1.00	1.00	1.00	1.00	5.00	1.00	1.00	1.00	1.00	1.71	1.71
Burrowing Owl	Gh7	4.00	5.00	2.00	3.00	3.00	5.00	4.00	3.00	2.00	3.00	3.57	3.86
Cedar Waxwing	Ts	2.00	3.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.14	2.29
Chestnut-collared Longspur	Gxh	3.00	3.00	4.00	4.00	4.00	3.00	4.00	3.00	2.00	3.00	3.29	3.57
Chipping Sparrow	Efs	1.00	3.00	4.00	2.00	1.00	1.00	4.00	3.00	4.00	3.00	2.00	2.00
Cliff Swallow	Pw45	2.00	2.00	4.00	2.00	1.00	1.00	3.00	3.00	3.00	3.00	2.00	2.00
Common Nighthawk	Eh	2.00	2.00	4.00	2.00	1.00	5.00	3.00	3.00	4.00	3.00	2.43	2.29
Common Yellowthroat	Wms1	1.00	3.00	2.00	2.00	1.00	2.00	4.00	3.00	5.00	2.00	2.29	2.14
Dickcissel	Ga9	2.00	3.00	3.00	2.00	3.00	5.00	5.00	1.00	4.00	3.00	3.29	3.43
Eastern Bluebird	Ec85	2.00	3.00	2.00	3.00	3.00	1.00	3.00	4.00	3.00	4.00	2.43	2.43
Eastern Kingbird	E	1.00	1.00	2.00	3.00	2.00	3.00	2.00	3.00	1.00	1.00	2.00	2.14
Eastern Phoebe	Td15	2.00	4.00	4.00	3.00	3.00	1.00	3.00	4.00	3.00	5.00	2.57	2.57
Ferruginous Hawk	Gxht7	4.00	4.00	3.00	3.00	3.00	4.00	3.00	3.00	3.00	3.00	3.43	3.43
Grasshopper Sparrow	Gxa	2.00	2.00	3.00	2.00	2.00	5.00	5.00	1.00	2.00	3.00	2.57	3.00
Gray Catbird	Sn12	2.00	4.00	2.00	2.00	2.00	1.00	4.00	2.00	2.00	3.00	2.29	2.57
Great Crested Flycatcher	Tdc1	2.00	4.00	3.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	3.00	3.00
Horned Lark	Gh7	1.00	1.00	1.00	1.00	1.00	5.00	2.00	2.00	2.00	3.00	1.71	1.71
House Wren	Tc1	1.00	2.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	2.00	1.29	1.29
Indigo Bunting	Tds1	1.00	3.00	3.00	2.00	3.00	1.00	3.00	4.00	3.00	4.00	2.29	2.29
Killdeer	Gh67	1.00	2.00	2.00	1.00	1.00	5.00	4.00	1.00	5.00	1.00	2.29	2.14
Lark Bunting	Gxhs	2.00	3.00	3.00	3.00	4.00	5.00	4.00	2.00	3.00	3.00	3.29	3.43
Lark Sparrow	E	3.00	2.00	3.00	2.00	2.00	2.00	3.00	3.00	1.00	2.00	2.14	2.43
Least Flycatcher	Td1	3.00	4.00	5.00	4.00	2.00	1.00	3.00	3.00	2.00	3.00	2.71	2.86

Appendix 2 (Continued).

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
Loggerhead Shrike	Es2	3.00	4.00	4.00	4.00	2.00	2.00	3.00	3.00	2.00	2.00	2.86	3.00
Long-billed Curlew	Gxh7	3.00	4.00	4.00	3.00	4.00	1.00	4.00	3.00	5.00	1.00	3.43	3.29
Long-eared Owl	Efo0	3.00	3.00	3.00	3.00	1.00	1.00	3.00	5.00	3.00	5.00	2.14	2.14
Marsh Wren	Wm	2.00	4.00	2.00	4.00	3.00	1.00	3.00	3.00	3.00	4.00	2.57	2.57
Mourning Dove	Ew	1.00	1.00	1.00	1.00	1.00	4.00	1.00	1.00	3.00	3.00	1.71	1.43
N. Rough-winged Swallow	Pw4	3.00	3.00	3.00	2.00	1.00	2.00	4.00	3.00	3.00	3.00	2.43	2.57
Northern Flicker	Ec8	1.00	2.00	1.00	1.00	1.00	2.00	4.00	2.00	3.00	3.00	1.57	1.71
Northern Harrier	Gasm	3.00	3.00	3.00	4.00	1.00	5.00	4.00	3.00	4.00	3.00	3.00	3.00
Northern Mockingbird	Eds12	1.00	2.00	2.00	1.00	2.00	1.00	3.00	4.00	3.00	4.00	1.71	1.71
Northern Oriole	Tdsl	2.00	3.00	3.00	2.00	2.00	2.00	3.00	3.00	3.00	3.00	2.43	2.43
Orchard Oriole	Tdsl	3.00	3.00	3.00	2.00	3.00	3.00	2.00	2.00	4.00	3.00	3.00	2.71
Red-eyed Vireo	Tdul	1.00	4.00	4.00	2.00	2.00	1.00	3.00	3.00	3.00	4.00	2.29	2.29
Red-tailed Hawk	Etg	1.00	2.00	2.00	2.00	1.00	5.00	3.00	3.00	3.00	3.00	2.14	2.14
Red-winged Blackbird	Wms1	1.00	2.00	1.00	1.00	1.00	3.00	4.00	2.00	4.00	3.00	1.86	1.86
Rock Wren	P4	3.00	3.00	2.00	2.00	3.00	1.00	4.00	2.00	4.00	3.00	2.57	2.57
Rufous-sided Towhee	Sn	1.00	3.00	4.00	2.00	2.00	2.00	4.00	3.00	4.00	3.00	2.29	2.29
Savannah Sparrow	Gx3	3.00	4.00	4.00	3.00	1.00	1.00	5.00	1.00	5.00	1.00	2.71	2.71
Say’s Phoebe	G45	3.00	2.00	3.00	3.00	2.00	1.00	3.00	3.00	3.00	3.00	2.43	2.43
Short-eared Owl	Gasm	3.00	3.00	4.00	4.00	1.00	5.00	2.00	3.00	4.00	3.00	3.00	2.71
Sprague’s Pipit (historic)	Gxa	3.00	5.00	5.00	3.00	4.00	0.00	3.00	3.00	3.00	3.00	3.00	3.00
Swainson’s Hawk	Gxt9	3.00	2.00	2.00	3.00	2.00	5.00	2.00	1.00	2.00	3.00	2.86	2.86
Tree Swallow	Ec15	2.00	3.00	3.00	3.00	1.00	1.00	2.00	3.00	3.00	3.00	2.14	2.00
Turkey Vulture (no nest?)	E4	1.00	2.00	4.00	2.00	1.00	1.00	2.00	2.00	4.00	3.00	1.71	1.43
Upland Sandpiper	Gx	3.00	2.00	3.00	3.00	3.00	5.00	2.00	3.00	3.00	3.00	3.74	3.00
Vesper Sparrow	Gxs	3.00	3.00	4.00	2.00	2.00	1.00	4.00	3.00	4.00	3.00	2.43	2.43
Warbling Vireo	Td1	2.00	4.00	4.00	2.00	2.00	2.00	5.00	1.00	4.00	3.00	2.71	2.86
Western Kingbird	E	1.00	1.00	2.00	2.00	3.00	3.00	1.00	1.00	1.00	2.00	2.14	2.14
Western Meadowlark	Gx7	1.00	2.00	2.00	3.00	2.00	5.00	3.00	3.00	3.00	3.00	2.43	2.43
Willow Flycatcher	Sn12	3.00	4.00	3.00	3.00	3.00	1.00	3.00	5.00	4.00	3.00	3.00	2.86
Yellow Warbler	Tdsl	1.00	4.00	3.00	2.00	1.00	2.00	2.00	3.00	2.00	3.00	1.86	1.86
Yellow-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	2.00	1.00	2.00	3.00	3.00	4.00	2.71	2.43
Yellow-breasted Chat	Sn12	2.00	3.00	3.00	3.00	2.00	1.00	3.00	3.00	1.00	1.00	2.14	2.43
Yellow-headed Blackbird	Wm	3.00	3.00	2.00	3.00	3.00	2.00	2.00	3.00	4.00	3.00	3.00	2.71

Greater Prairie Chicken Nesting Habitat, Sheyenne National Grassland, North Dakota

Clinton McCarthy[1], Tim Pella[2], Greg Link[3], and Mark A. Rumble[4]

Abstract.-Greater prairie chicken *(Tympanuchus cupido pinnatus)* populations and habitats have declined dramatically in the Great Plains. The Sheyenne National Grassland (SNG) has the largest population of greater prairie chickens in North Dakota, but this population has declined over the past 15 years. Lack of nesting habitat has been identified as a significant factor contributing to the decline in greater prairie chicken populations throughout their range. We used the Habitat Suitability Index (HSI) model for greater prairie chickens to evaluate the nesting habitat conditions on the SNG. This population of greater prairie chickens appears to sustain itself on the brink of extirpation by nesting in the few areas that provide nesting cover and in private alfalfa fields. Encroachment of woody plants into the SNG, changes in private land-use patterns, removal of forage by domestic livestock contribute to the low suitability of the SNG for nesting by greater prairie chickens.

INTRODUCTION

The Sheyenne National Grassland (SNG) is approximately 28,745 ha of federally administered prairie in southeastern North Dakota. Within its administrative boundary there are an additional 25,910 ha of interspersed private cropland and prairie. The SNG contains the largest population of greater prairie chickens *(Tympanuchus cupido pinnatus)* in the state of North Dakota (Kobriger et al. 1987). Greater prairie chickens are not native to the SNG, but are considered a naturalized immigrant in North Dakota (Johnson and Knue 1989). Prairie chickens apparently moved into North Dakota from the north-central part of the United States during the Euro-American settlement in the 1870's and 1880's (Johnson and Knue 1989, Evans 1968). Greater prairie chicken populations and their habitats (native tall grass prairie) have declined to a small fraction of their historical range (Hjertaas et al. 1993, Samson and Knopf 1994). Thus, the population of greater prairie chickens on the SNG has both regional and national importance.

Numbers of prairie chickens on the SNG increased from the early 1960's through the early 1980's (Kobriger et al. 1987). Since then, prairie chicken numbers on the SNG have declined from a high of 410 males in 1983 to a low of 84 males in 1994 (Kobriger et al. 1987, unpubl. data, Sheyenne National Grassland, Lisbon, ND). State and federal natural resource management agencies, and conservation groups are concerned that management of the SNG may be contributing to the decline in the greater prairie chicken population. Lack of suitable nesting habitat has been identified as the most significant factor limiting populations of greater prairie chickens across their range (Kirsch 1974, Westemeir 1973) and in North Dakota (Svedarsky 1979).

Habitat suitability index (HSI) models are an accepted method for quantifying species' habitats as numerical index (Schamberger et al. 1982). Biological and habitat information are synthesized to formulate index values between zero (unsuitable) and one (optimum) for habitat requisites considered important to a species (U.S. Fish and Wildlife Service 1980). We conducted HSI analyses to assess habitat conditions for greater prairie chickens on the SNG at three scales: 1) the western portion of the SNG and adjacent private lands, 2) the Durler/Venlo Management unit, and 3) areas $\leq$1.6 km of the 14 active booming grounds.

METHODS

The HSI model for greater prairie chickens (Prose 1985) identifies two habitat components, nesting cover and winter food, as the most important habitat

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ponents for prairie chickens. The HSI for nesting cover is based on grassland vegetation height/density (expressed as visual obstruction measurements on a pole, Robe1 et al. 1970) for nesting cover in the spring (figure 1).

We mapped the lowland, midland, and upland grassland vegetation types (Manske and Barker 1987) on 1:24,000 aerial photos of the SNG. Most nesting by greater prairie chickens on the SNG occurs within 1.6 km of leks (Newell et al. 1987). The Custer National Forest Land Management Plan (U.S. Forest Service, Custer National Forest, Billings, MT, 1986) requires that nesting habitat for prairie grouse be assessed within 1.6 km of leks. During October and November, 1994, we estimated height/density of vegetation in these vegetation types from 81 transects within 1.6 km of greater prairie chicken leks in the northern and western portion of the SNG. At each of 10 stations on each transect, we recorded the height that vegetation obstructed 100 percent of a pole (VOR) marked in 0.5 dm increments when viewed from four directions (at 90” azimuths) at a distance of 4 m and a height of 1 m from the pole (Robelet al. 1970). VORs were averaged for each station and the average among stations was used to estimate transect VORs. We placed six transects in upland vegetation, 51 transects in midland vegetation and 26 transects in lowland vegetation. Data from these transects were used as VOR estimates in the mapped vegetation polygons they were collected in. For all other mapped vegetation polygons, these VOR data served as calibrations for ocular estimates of five VOR classes (0 - 0.50 dm, 0.51 - 1.0 dm, 1.01 - 1.5 dm, 1.51 - 2.0 dm, and >2.0 dm) during field reconnaissance. Maps of vegetation and VOR class assignments were transferred to 1:24,000 U.S. Geological Survey maps and the area of each vegetation was planimetered for use in the HSI estimates.

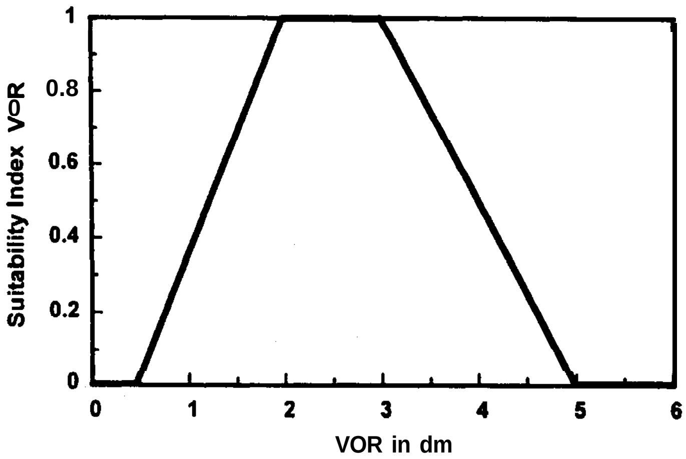

Figure 1. Relationship between average 100 percent obstruction of pole (VOR) marked in 0.5 dm increments and next cover suitability index for greater prairie chickens (from Prose 1985).

HSI for nesting cover is estimated in three steps (Prose 1985). First, a suitability index is estimated from the midpoint of the VOR classes of each vegetation type i (SI_{VORi}). Second, the percent of area providing equivalent optimal nesting habitat (EONH) is calculated using:

$$EONH = \sum_{i=1}^{n} (SI_{VOR_i})(N_i)$$

where n = total number of vegetation types, and N = percent of the area in vegetation type i. Third, HSI for nest cover is calculated from:

$$HSI = \frac{(0.735 * EONH) - 21.4}{37}$$

Characteristics of vegetation and winter snow accumulation influence the structure of vegetation in the spring for nesting by greater prairie chickens. VOR measurement collected in the fall decrease prior to spring nesting. This decrease is proportional to the height of vegetation and for the range of VOR 0.5 - 2.0 dm varies from 7-40 percent in mixed grass prairie (G. Schenbeck pers. commun., Nebraska National Forest, Chadron, NE). Over winter VOR losses on the SNG are probably different, but data are lacking. We selected 15 percent over-winter VOR losses to estimate spring nesting cover based on fall VOR estimates because the VORs for the SNG are near the lower end of the range.

Western SNG Analysis

The western part of the SNG includes most of the prairie chicken leks. This area included 3433 ha of private land and 8984 ha of SNG administered lands. We calculated the HSI for this analysis unit to show estimated contributions to the HSI for prairie chickens from adjacent private lands. VOR class tion was available for only 5738 ha (64 percent) of the SNG lands in this analysis unit. We assumed the mapped VOR classes were representative of the remaining of the western SNG and used these data for HSI calculations in this analysis unit. For private lands in the western SNG analysis unit we assumed: 1) CRP land had VOR class > 2.0 dm; 2) hay and alfalfa had VOR cover classes <0.5 dm because of mowing approximately the third week of June that destroys existing nests and most young hatched birds; and 3) grazed pasture had VOR cover class 0.51-1.0 dm.

Durler/Venlo Management Unit

The Durler/Venlo management unit includes 3645 ha in nine range management allotments in the western SNG. The Durler/Venlo unit is a subset of the prairie chicken range in the western portion of the SNG. It includes the larger leks, highest prairie chicken numbers, and the greatest number of prairie chicken leks not shared by sharp-tailed grouse (*Tympanuchus phasianellus jamesi*). Most of the Durler/Venlo management unit is< 1.6 km from a prairie chicken lek. This portion of SNG has complete vegetation classification and mapping.

We excluded vegetation communities that were not available for nesting by greater prairie chickens from the HSI for the Durler/Venlo management unit. This HSI analysis presents a complete picture of the nesting habitat for this area. We assigned vegetation types to mapped polygons using the dominant vegetation community in the polygons. Within these polygons, vegetation communities not capable of producing 1.5 dm VOR measurements or that are usually flooded (Manske and Barker 1987, Newell et al. 1987) were considered unavailable for nesting by greater prairie chickens. The area in each polygon assigned to a VOR class did not include unsuitable areas. For example, lowland vegetation communities dominated by species such as *Carex lanulosa* were considered unavailable because in most years the ground is flooded. Upland vegetation communities dominated by species such as *Boutelou gracilis* were considered unavailable for prairie chicken nesting because they are not capable of producing at least 1.5 dm VOR in most years.

Area Surrounding 14 Active Leks

The area within 1.6 km of active leks includes most of the nesting habitat of greater prairie chickens. This scale of analysis allowed us to evaluate HSI for areas of known greater prairie chicken occurrences. This level of analysis included the area surrounding active greater prairie chicken leks and we expected HSI from this analysis should equal or exceed the HSI's from the blocks of SNG that included areas > 1.6 km from leks and unused areas.

RESULTS

Western Sheyenne National Grassland

The 12,445 ha in the western SNG had 24 percent EONH (table 1), less than the minimum considered necessary for the HSI to be greater than zero using fall VOR estimates. When over-winter VOR losses were included, the EONH in the spring declined to 21 percent, with an HSI remaining zero.

Durler/Venlo Management Unit

EONH in the Durler/Venlo unit was lower that the western SNG. EONH was reduced by eliminating the lowlands that are usually flooded in the spring from the HSI calculations. The net result was 12 percent fall EONH and 9 percent EONH in the spring. The subsequent HSI for the Durler/Venlo unit was also zero.

Table 1. Percent equivalent optimal nesting habitat and nesting HSI for three analysis areas with and without winter VOR loss on the Sheyenne National Grassland.

Analysis area	Percent EONH[1]	HSI	Percent EONH with overwinter VOR loss	HSI
Western SNG	23.8	0	19.8	0
Durler/Venlo	11.7	0	9.3	0
≤1 .6 km leks	25.7	0	21.1	0

[1] EONH = equivalent optimum nesting habitat as defined in HSI model by Prose 1985).

Area Surrounding 14 Active Leks

The area within 1.6 km of the 14 active leks had a larger EONH (26 percent) in the fall than the other analysis units. However, the nesting HSI was zero for this area as well. Four of the lek areas provided sufficient EONH for HSI's greater than zero. However HSI estimates for spring showed that only two of these leks still provided sufficient EONH for HSI's greater than zero.

DISCUSSION

Nesting HSI

Our data suggests that nesting cover limits greater prairie chicken populations on the SNG. HSI's were zero for all the analysis units we compared. Four leks had sufficient nesting cover in the surrounding 1.6 km for HSI's greater than zero based on the fall measurements. HSI for these lek areas were less than 0.2 Only two leks had HSI's greater than zero for the area within 1.6 km from leks after over winter VOR losses were considered. HSI's for these two leks were ≤ 0.1

VOR measurements in grassland vegetation that are 2 to 3 dm are considered optimal nest cover for greater prairie chickens (Prose 1985). VOR measurements > 1.5 dm provide $SI_{VOR} > 0.7$. Only 16 percent of the western SNG was in the VOR class > 1.5 dm. In the Durler/Venlo management unit, only 7 percent of the suitable nesting area provided vegetation > 1.5 dm. For areas (1.6 km of leks, only 14 percent of the area had vegetation in the >1.5 dm VOR classes. Suitable nesting cover for prairie chickens may increase during drought years because lowlands that are usually flooded are drier and usable for nesting by hens.

Most of the nesting habitat for greater prairie chickens in the SNG is the midland community type in the humocky sandhills (Manske and Barker 1981, Manske and Barker 1987). Switchgrass *(Panicum virgatum)* communities found on the toe slopes surrounding lowland meadows provide the primary prairie chicken nesting cover on the SNG (Manske and Barker 1987, Newell 1987). Although lowlands are not considered suitable for nesting in most years, the lowland/midland interface is used for nesting by prairie chickens (Newell 1987). The lack of adequate cover for nesting in upland communities was attributed to heavy livestock utilization (Newell 1987). Historically, upland communities were likely tall grass prairie (Burgess 1964), but currently have limited capacity to provide nesting cover because they are dominated by short cool season and warm season grasses such as Kentucky bluegrass and blue grama.

The HSI model (Prose 1985) assumes that optimum nesting habitat conditions exist when 80 percent of the area supports herbaceous vegetation with a VOR of 2 - 3 dm. However, lingering populations of greater prairie chickens can exist in areas with 10-15 percent permanent grassland (Hamerstrom et al. 1957, Prose 1985). Topfer et al. (1990) considers a spring population of 200 birds (100 males) as a minimum number to insure perpetuation of the population. Greater prairie chickens probably persist on the SNG because natural variation provides small limited areas with adequate nesting cover. These areas exist at the lowland/midland community interface, in lowlands during drought years, and in limited quantity surrounding some leks. Limited nesting also occurs in alfalfa on private lands (Newell 1987). Small populations, such as the greater prairie chicken on the SNG, are highly susceptible to extinction due to catastrophic natural events (Ruggiero et al. 1994).

Robustness of Analyses to Assumptions

Because the HSI in our evaluation were based on ocular estimates of VOR classes, we conducted analyses to estimate HSI for systematic errors in estimating the VOR classes. If we over estimated the VOR classes (e.g.,VOR was actually lower), then HSI would decline further. Because, the lower limit on HSI is zero, our conclusion of limited nesting habitat remained unchanged.

If we systematically underestimated VOR classes by one class (0.5 dm), HSI for the Western SNG increased to 0.1 for fall VOR estimates and remained zero for estimates of spring nesting cover. HSI in the Durler/Venlo unit remained zero for both spring and fall VOR estimates. HSI for the areas around active leks increased to 0.3 for fall VOR estimates, but declined to 0.1 for spring estimates of nesting cover. Because the area surrounding leks included lowlands that are flooded in most years, the HSI was probably lower. None-the-less, analyses that assume we underestimated nesting cover, still show that nesting habitat is limited on the SNG.

The VOR estimates we used for the 3433 ha private lands in western SNG analysis unit were made subjectively post hoc. Because, these post hoc estimates of private land VOR may have influenced the HSI, we conducted an analysis that would present the best possible HSI for this analysis unit. HSI for the western SNG was recalculated assigning all private lands with suitable vegetation types (hay and alfalfa, pastures, and CRP) for nesting, a SI_{VOR} of 1.0 (this analysis does not change the HSI for nest cover on lands managed by the SNG). The resulting HSI for nest cover increased for the western SNG analysis unit to 0.33. This HSI represents the upper limit for the western SNG analysis unit, but it is not realistic. Most of the area considered to have SI_{VOR} of 1.0 are grazed or mowed annually. Hay and alfalfa is usually cut by the third week of June, destroying existing nests and young broods unable to escape the mowers. Only the 251 ha of CRP in the analysis unit maintained its structural integrity throughout the nesting and brood rearing periods. None-the-less, this analysis still indicated that regional nesting habitat for greater prairie chickens is limited in the vicinity of the SNG.

Contributing Factors

The encroachment of woody and exotic plant species, changes in adjacent agricultural/land use changes, and livestock grazing practices are three human induced factors that directly or and indirectly influence nesting cover for prairie chickens on the SNG. Quaking aspen *(Populus tremuloides)*, willow *(Salix* spp.) and Russian olive *(Elaeagnus angustifolia)* have encroached into prairie reducing nesting cover on the SNG (Kobriger et al. 1987, Jensen 1992). Leafy spurge *(Euphorbia esula)* has expanded from 7 percent to over 17 percent of the SNG since 1985 (unpubl. data, SNG). Encroachment of woody plants reduces and fragments suitable nesting, brood rearing and roosting cover (Svedarsky 1979); provides travel corridors and perch sites for predators (Burhnerkempe et al. (1984) and creates habitat more suitable for closely related sharp-tailed grouse (Prose 1987).

Agricultural development on private lands adjacent to the SNG over the past 10-15 years shows that remnant prairie habitats on private lands have been largely converted to croplands (unpubl. data, Nat. Res. Conserv. Serv., Lisbon, ND). Our analysis of the western SNG unit, showed that most of the suitable nesting habitat on private lands was Conservation Reserve Program comprising 250 ha in the analysis unit. No privately owed parcels of native prairie were identified in our analysis of the western SNG.

Grazing by livestock is the predominant use of the SNG. Livestock stocking rates have fluctuated between 50,000 and 60,000 AUMs over the past 10 - 15 years on the SNG. However, the size of livestock has increased approximately 40 percent during a comparable period (L. Potts, pers. commun., SNG, Lisbon, ND). These heavier animals require approximately 30 percent more forage (National Research Council 1984) than the standard AUM established for a 454 kg animal.

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LITERATURE CITED

Burgess, R. L. 1964. Ninety years of vegetational change in a township in southeastern North Dakota. Proc. North Dakota Acad. Sci. 18:84-94.

Burhnerkempe, J. E.; Edwards, W. R.; Vance, D. R.; Westemeir, R. L. 1984. Effects of residual vegetation on prairie chicken nest placement and success. Wildl. Soc. Bull. 12:382-386.

Evans, K. E. 1968. Characteristics and habitat requirements of the greater prairie chicken and sharp-tailed grouse: a review of the literature. Cons. Res. Rep. No. 12. Fort Collins, CO: U. S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 32 p.

Hamerstrom, F. N. Jr; Mattsen, 0. E.; Hamerstrom, F. 1957. A guide to prairie chicken management. Tech. Bull. 15. Madison, WI: Wisconsin Conservation Department. 128 p.

Hjertaas, H; et al. 1993. National recovery plan for the greater prairie chicken. Renewable Rep. No. 5, Ottawa, Ontario: Canadian Wildlife Federation. 18 p.

Jensen, W. F. 1992. Historical review of prairie chicken management on the Sheyenne National Grassland. Unpublished Report. Bismarck, ND: North Dakota Game and Fish Department.

Johnson, M. D.; Knue, J. 1989. Pinneated grouse. In: Feathers from the prairie. Bismarck, ND: North Dakota Game and Fish Department: 97-122.

Kirsch, L. M. 1974. Habitat management considerations for prairie chickens. Wildl. Soc. Bull. 2:124-129.

Kobriger, G. D.; Vollind, D. I?; McNeill, M. E.; Higgins, K. F. 1987. Prairie chicken populations of the Sheyenne Delta North Dakota 1961-1987. pp. 1-7. In: A. J. Bjugstad, tech. coord. Prairie Chickens on the Sheyenne National Grasslands. Gen. Tech. Rep. RM-159. Fort Collins, CO: U. S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station. 73 p.

Manske, L. L.; Barker, W. T. 1981. The prairie grouse on the Sheyenne National Grasslands. Unpublished Report. Fargo, ND: North Dakota State Univ. 238 p.

Manske, L. L.; Barker, W. T. 1987. Habitat Usage by prairie grouse on the Sheyenne National Grasslands. pp. 8-20. In: A. J. Bjugstad, tech. coord. Prairie Chickens on the Sheyenne National Grasslands. Gen. Tech. Rep. RM-159. Fort Collins, CO: U. S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station. 73 p.

National Research Council. 1984. Nutrition requirements for beef cattle, sixth revised edition. Washington, D. C.: National Academy Press. 90 p.

Newell, J. A. 1987. Nesting and brood rearing ecology of the greater prairie chicken in the Sheyenne National Grasslands, North Dakota. Boseman, MT: Montana State University. 111 p. M. S. thesis.

Newell, J. A.; Toepfer. J. E.; Rumble; M. A. 1987. Summer brood rearing ecology of the greater prairie chicken on the Sheyenne National Grasslands. pp. 24-31. In: A. J. Bjugstad, tech. coord. Prairie Chickens on the Sheyenne National Grasslands. Gen. Tech. Rep. RM-159. Fort Collins, CO: U. S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station. 73 p.

Prose, B. L. 1985. Habitat suitability index models: greater prairie chicken (multiple levels of resolution). Biol. Rep. 82 (10.102). Fort Collins, CO: U. S. Department of Interior, Fish and Wildlife Service. 33 p.

Prose, B. L. 1987. Habitat suitability index models: plains sharp-tailed grouse. Biol. Rep. 82(10.142). Fort Collins, CO: U. S. Department of Interior, Fish and Wildlife Service. 31 p.

Robel, L. J.; Briggs, J. N; Dayton, A. D.; Hulbert, L. C. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. J. Range Manage. 23:295-297.

Ruggiero, L. F.; Hayward, G. D.; Squires, J. R. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population and ecological scale. Conserv. Biol. 8:364-372.

Toepfer, J. E.; Eng, R. L.; Anderson, R. K. 1990. Translocation of prairie grouse: what have we learned? Trans. N. Amer. Nat. Resour. Conf. 55:569-579.

Samson, F.; Knopf, F. 1994. Prairie conservation in North America. Bioscience 44:418-421.

Shamberger, M. A.; Farmer, A. H.; Terrell, J. W. 1982. Habitat suitability index models: introduction. FWSI OBS-82/10. Fort Collins, CO: U. S. Department of Interior, Fish and Wildlife Service. Western Energy and Land Use Team. 2 p.

Svedarsky, W. D. 1979. Spring and summer ecology of female greater prairie chickens in northwestern Minnesota. Grand Forks, ND: University of North Dakota. 166 p. Ph. D. dissertation.

Westemeir, R. L. 1973. Prescribed burning in grassland management for prairie chickens in Illinois. In: Proceeding, 12th annual Tall Timbers Fire Ecology Conference. June 8-9, 1972. Lubbock, TX. Tallahassee, FL: Tall Timbers Research Station; 12:317-338.

U. S. Fish and Wildlife Service. 1980. Habitat as the basis for environmental assessment. Ecol. Serv. Man. 101, Release 4-80. Washington, D. C.: U. S. Department of Interior, Fish and Wildlife Service, Division of cal Services.

Black-Tailed Prairie Dog Status and Future Conservation Planning

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Abstract.-The black-tailed prairie dog is one of five prairie dog species estimated to have once occupied up to 100 million ha or more in North America. The area occupied by black-tailed prairie dogs has declined to approximately 2% of its former range. Conversion of habitat to other land uses and widespread prairie dog eradication efforts combined with sylvatic plague, Yersinia pestis, have caused significant reductions. Although, the species itself is not in imminent jeopardy of extinction, its unique ecosystem is jeopardized by continuing fragmentation and isolation.

INTRODUCTION

The black-tailed prairie dog, Cynomys *ludovicianus* Ord, is the most widespread and abundant of five species of prairie dog in North America. Two species, the Utah prairie dog, C. *parvidens* J.A. Allen and the Mexican prairie dog, C. *mexicanus,* are currently listed as threatened and endangered, respectively, under the Endangered Species Act of 1973. The two other widespread species are the white-tailed prairie dog, C. *leucurus* Merriam and the Gunnison's prairie dog, C. *gunnisoni* Baird.

The black-tailed prairie dog is native to the short and midgrass prairies of North America. Its historic range stretches from southern Canada to northern Mexico and includes portions of Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming (Hall and Kelson 1959). The eastern boundary of prairie dog range is approximately the western edge of the zone of tallgrass prairie, from which prairie dogs are ecologically excluded. The western boundary of this species is roughly the Rocky Mountains. Its range is contiguous with, but generally does not overlap, ranges of other prairie dog species.

With the exception of Arizona, from which it has been extirpated, the species still occurs in all the states (including Canada and Mexico) within its historic range. Yet, widespread reductions have occurred in population numbers and occupied areas throughout this broad range. Historic evidence suggests that the total area occupied by all species of prairie dogs may have declined by as much as 98% during the first half of this century (Miller et al. 1994).

METHODS

We sent letters of inquiry to state and federal conservation and land management agencies and consulted published reports. This information was augmented by telephone interviews with individuals knowledgeable about prairie dog management. The area surveyed included all states within the original range of the black-tailed prairie dog. Although responses were received from all states and agencies queried, the quality of survey information varied. Therefore, this report is a picture of prairie dogs in the mid-1980s rather than an accurate assessment of 1995 populations.

Prairie dog abundance and distribution is probably better documented at present than at any previous time due to improved mapping techniques and greater interest in prairie dogs by land management agencies. Yet, prairie dog occupied acreage can still only be grossly estimated. A primary factor contributing to this uncertainty is that much of the mapping effort is temporally distributed over a decade or more and there is no method available to assess prairie dog abundance over a broad area within a short span of time. Typically, prairie dog populations change substantially within a few years due to the threats discussed below and to climatic factors and prairie dog reproductive ecology. Another factor contributing to errors in determining prairie dog abundance is a lack of information from private and state lands.

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THREATS TO THE PRAIRIE DOG

A number of causes have been identified or proposed to account for the reductions in the acreage occupied by black-tailed and other prairie dog species. We believe that four areas of threat warrant further discussion: 1) loss of habitat due to conversion of prairie to other land uses; 2) intentional poisoning or other eradication or control efforts, primarily prompted by the livestock industry; 3) shooting for recreation or as a control effort; and 4) sylvatic plague, *Yersinia pestis.*

LOSS OF PRAIRIE

Prairie dominated by blue grama, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths, and buffalograss, *Buchloe dactylides* (Nutt.) Engelm., possibly due to its relatively flat topography, is among the first grassland converted to.agriculture (Dinsmore 1983). As a result, Graul (1980) noted that as much as 45% of this prairie type has been lost to other land uses. Reductions in all shortgrass and midgrass prairies is expected to be similar or possibly greater in some midgrass regions where precipitation may be more suitable for agriculture. Although National Grassland acreage in the northcentral region of the Forest Service represents only about 5% of that agency's land base, it also represents the majority of the native prairie remaining in this region of North and South Dakota (Knowles and Knowles 1994).

Currently, with the exception of some areas of the northwestern portion of the black-tailed prairie dog's range, conversion of prairie to agricultural has lessened. This is because much of the arable land is already in cultivation or has been converted to non-native grasses for forage. Municipal and industrial development probably account for most of the present losses to native prairies in the United States. While these losses are minor compared with those that occurred during settlement of this country, they continue to reduce habitat availability for prairie dogs and other species.

ERADICATION OR CONTROL EFFORTS

Eradication efforts have been carried out against prairie dogs on a very large scale, affecting several million ha of land (Anderson et al. 1986; Bell 1921). Clark (1979) reported that in some years prairie dogs were intentionally poisoned on more than 8 million ha in the United States. During the early 1980s, 185,600 ha of prairie dogs were eradicated on the Pine Ridge Indian Reservation in South Dakota (Hanson 1988; Sharps 1988). In 1986 and 1987, a South Dakota black-tailed prairie dog complex of 110,000 ha was destroyed, eliminating the largest remaining complex in the United States (Tschetter 1988).

Virtually every federal land management agency has been involved in this effort. The U.S. Fish and Wildlife Service used compound 1080 until its ban in 1972. In 1976, this agency approved the use of zinc phosphide as a prairie dog control agent, hoping to avoid secondary poisoning of nontarget species while maintaining its prairie dog poisoning program. It is estimated that permitting activities by both the Environmental Protection Agency and the Animal and Plant Health Inspection Service account for the annual poisoning of 80,000 ha of prairie dogs in the United States (Captive Breeding Specialist Group 1992). Much of this effort occurs on federally-owned and managed land, despite the fact that less than 5% of the United States beef weight is produced on these lands (United States General Accounting Office 1988). Most poisoning on federal land is due to private land concerns, not necessarily federal forage concerns.

The legal designation indicating the regulatory status of the black-tailed prairie dog varies among the 10 states in which it still occurs. In four states the species is designated a legal agricultural pest, with some level of either state or local mandatory controls in effect. This includes statewide legislation mandating control of prairie dogs in Wyoming. In Colorado, Kansas, and South Dakota, state legislation allows counties or townships to mandate controls on landowners. In 1995, Nebraska repealed their long-standing legislation that mandated statewide control, thereby joining the states of Montana, New Mexico, North Dakota, Oklahoma, and Texas, where control is not mandatory but assistance may be provided to landowners who believe they have a prairie dog population problem that requires control.

PRAIRIE DOG SHOOTING

Shooting of prairie dogs, either for recreation or to reduce or control their numbers, is widespread across the range of all species in the United States.

The impact this activity has on overall populations remains unclear, but preliminary monitoring results by the Bureau of Land Management (BLM) in Montana indicate that some level of shooting might impact the growth and expansion of prairie dog colonies (Reading et al. 1989). Fox and Knowles (1995) suggested that persistent unregulated shooting over a broad area of the Fort Belknap Indian Reservation in Montana might have significantly influenced prairie dog populations. However, they further concluded that it would require approximately one recreational day of shooting for every 6 ha of prairie dogs to result in such an impact. This level of shooting pressure is unlikely over the hundreds of thousands of ha of currently occupied range.

SYLVATIC PLAGUE

Prairie dogs have coexisted with a variety of predators for many centuries on the plains and have adapted means of persisting in spite of this predation. However, a more recent threat has arrived to which the prairie dog has no adaptive protection. A flea-borne bacterium, the sylvatic plague, was introduced into North America just before the turn of the century. First discovered in black-tailed prairie dogs in Texas in the 1940s (Cully 1989), small rodents such as prairie dogs apparently have no natural immunity to the plague, which now occurs virtually throughout the range of the black-tailed prairie dog.

The impacts of plague are more adverse than just the killing of many individuals. The plague persists in a colony resulting in a longer population recovery time than is common in colonies that have been poisoned (figure 1). Four years following impact, plague-killed colonies on the Rocky Mountain Arsenal National Wildlife Refuge had recovered to only 40%, while poisoned colonies had recovered to over 90% (Knowles 1986). Knowles and Knowles (1994) suggested that prairie dogs have survived the introduction of this disease simply due to their large, highly dispersed populations. Further reductions in these populations could make prairie dogs much more susceptible to local or regional extirpations due to the plague.

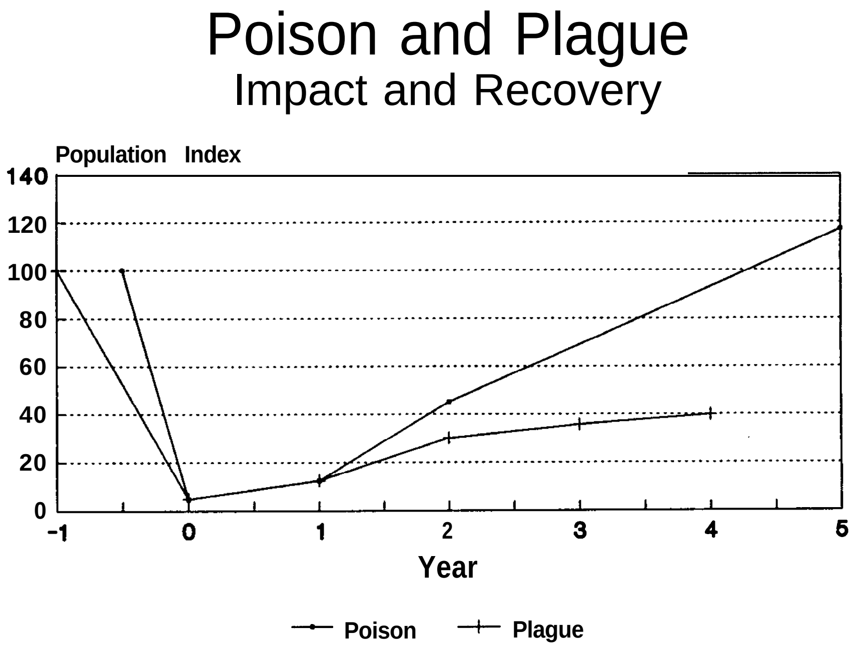
Poison and Plague
Impact and Recovery

Figure 1. Comparison of prairie dog population recovery at the Rocky Mountain Arsenal National Wildlife Refuge following plague and at two colonies following control with zinc phosphlde (Knowles 1986).

HISTORIC AND CURRENT STATUS

Rangewide

Seton (1929) estimated that in the early part of this century, there may have been 5 billion prairie dogs in North America. Around that time, prairie dog colonies were estimated to occupy 40 million to 100 million ha of prairie in North America, but by 1960 this area was reduced to approximately 600,000 ha (Anderson et al. 1986; Marsh 1984). These estimates result in the often-cited figure of a 98% decline in population among the five species of prairie dog. So, while the black-tailed prairie dog still occurs in all but one of the states in its historic range, significant reductions in its total colony area have taken place rangewide.

Table 1. Historic 920) and recent (post-1980) estimates of total area (ha) occupied by black-tailed prairie dogs in the United States.

State	Historic	Recent	% Chancre
AZ	[1]	extirpated	-100
co	2,833,000		
KS	810,000	18,845	-98
MT	595,000	35,545	-94
NE		24,415	[1]
NM[2]	4,838,460	201,220	-96
ND	85,000	8,500	-90
OK		3,850	[1]
SD	711,000	100,000	-86
TX	23,000,000	12,145	-99.9
WY		82,590	-75
United States	40,000,000 to 100.000.000	550,000	-98 to -99

[1] *Reliable data unavailable for analysis.*

[2] *Includes black-tailed and Gunnison's prairie dogs.*

PRAIRIE DOG STATUS IN EACH STATE

Current status information was solicited from state and federal agencies and from tribal authorities in all eleven states in the historic range of the black-tailed prairie dog (table 1). The following summary provides updated status and population data for those states.

Arizona

The Arizona Game and Fish Department (Duane L. Shroufe, Director, *in litt.* 1995) confirms that the black-tailed prairie dog, in the form of the Arizona subspecies C. *ludovicianus arizonensis*, is extirpated from the state. However, it still occurs nearby in Mexico and New Mexico. Arizona still supports populations of Gunnison's prairie dogs.

Colorado

On the Comanche and Pawnee National Grasslands, the Forest Service *(in litt.)* currently estimates a total of 2,455 ha of active prairie dogs, compared with 910 ha from 1978 to 1980 (Schenbeck 1982). This represents more than a doubling in area, but also represents only 0.5% of the area available on these public lands. Bent's Old Fort National Historic Site contains 325 ha of black-tailed prairie dogs (NPS, *in litt.).* Fort Carson and surrounding private lands contain approximately 1,620 ha, Pinyon Canyon less than 810 ha of prairie dogs (FWS, *in litt.).* The Rocky Mountain Arsenal NWR (FWS, *in litt.)* prairie dog population declined from 1,850 ha to 100 ha between 1988 and 1989, due to plague. Burnett (1918) estimated that three combined species of prairie dog occupied 5,665,720 ha in Colorado in the early 1900s. Based on geographic distribution of black-tailed, white-tailed, and Gunnison's prairie dogs in the state, it may be assumed that black-tailed prairie dogs accounted for approximately half this figure. There is no reliable estimate of the total area occupied by black-tailed prairie dogs statewide at this time.

Kansas

The National Park Service *(in litt.)* reports approximately 16 ha of prairie dogs at the Fort Larned National Historic Site. On the Cimarron National Grassland, the Forest Service *(in litt.)* currently estimates 440 ha of active prairie dog colonies compared with 20 ha estimated from 1978 to 1980 (Schenbeck 1982). This represents more than a twenty-fold increase on this 44,000-ha area, yet still only 1% of the total area of the Grassland. Both Lee and Henderson (1988) and Powell and Robe1 (1994) reported that selected counties had reductions of 84% since the beginning of the century (Lantz 1903, cited in Lee and Henderson 1988). A survey completed in 1992

(Vanderfoof et al. 1994) estimates 18,845 ha of prairie dogs in Kansas, just over 2% of the 810,000 ha estimated by Lantz (1903) some 90 years ago.

Montana

Flath and Clark (1986) estimated that black-tailed prairie dogs occupied 595,000 ha of land in Montana from 1908 to 1914. Estimated prairie dog occupied area by the early 1980s had declined to 50,600 ha (Flath and Clark 1986) and subsequent estimates show further declines in prairie dogs (40,500 ha, Campbell 1986; 35,545 ha, FaunaWest Wildlife Consultants 1995). This most recent estimate indicates a statewide reduction in occupied area of approximately 94% since the early 1900s.

Nebraska

On the Oglala National Grassland and Nebraska National Forest, the Forest Service *(in litt.)* currently estimates 105 ha of active prairie dog colonies, compared with 145 ha estimated from 1978 to 1980 (Schenbeck 1982). Current estimates represent 1.4% of land available. In 1973, prairie dog occupied area in Nebraska was estimated at 6,075 ha (Lock 1973). By 1982, this figure had increased to an estimated 32,400 ha (Frank Andelt, Nebraska Game and Parks Commission, cited in FaunaWest Wildlife Consultants 1995). By 1989, prairie dogs statewide occupied approximately 24,415 ha (Kevin Church, Nebraska Game and Parks Commission, *in litt.).* Plague and increased eradication efforts, resulting from state legislation mandating prairie dog control, have reduced this figure significantly since the 1980s, with less than 0.22% of the Nebraska landscape currently occupied by the species (FaunaWest Wildlife Consultants 1995). Historic estimates are unavailable.

New Mexico

The BLM *(in litt.)* reports that prairie dogs may be extirpated from several sites, with only 140 ha remaining on BLM land in the state. The White Sands Missile Range (Department of Army, *in litt.)* contains just over 300 ha of prairie dogs. Around 1919 the area in New Mexico occupied by prairie dogs, both Gunnison's and black-tailed (including *C. l. arizonensis),* was approximately 4,838,460 ha, but was estimated to have been reduced to 201,220 ha by 1980 (Hubbards and Schmitt 1984). This is a 96% reduction. Hubbards and Schmitt (1984) further estimated that the range of the black-tailed prairie dog in New Mexico has been reduced by one-fourth, primarily from the range of *arizonensis.*

North Dakota

Theodore Roosevelt National Park reportedly contains less than 360 ha of prairie dogs (NPS, *in litt.),* approximately 1% of the total Park land area. There are believed to be currently 2,690 ha of prairie dogs on the 660,435 ha of Custer National Forest in North and South Dakota (Forest Service, *in litt.).* This represents 0.4% prairie dog occupancy of these lands. The Forest management plan calls for an occupancy level at or around 2,225 ha. The North Dakota Game and Fish Department *(in litt.)* reports approximately 8,300 ha of prairie dogs statewide, which may be a reduction of 90% or more from historic levels. In 1992, only six complexes of over 400 ha were identified.

Oklahoma

The Department of the Army *(in litt.)* has no current estimate of prairie dog areas on Fort Sill, but report that they have declined markedly in the past 10 years. Shackford et al. (1990) reported a statewide estimate of 3,850 ha in 1967, increasing by 93% to 7,440 ha in 1989.

South Dakota

On the Buffalo Gap and Fort Pierre National Grasslands, the Forest Service *(in litt.)* estimates 3,025 ha of active prairie dog colonies and an additional 2,600 ha of colonies are subject to periodic rodenticide treatments. This compares to 17,600 ha estimated from 1978 to 1980 (Schenbeck1982). The 500,285 ha Black Hills National Forest and Custer and Elk Mountain Ranger Districts currently support 53 ha of prairie dogs. In the early 1920s there may have been 711,000 ha of prairie dogs statewide (FaunaWest Wildlife Consultants 1995). The South Dakota Animal Damage Control office currently estimates 80,000 to 100,000 ha of active prairie dog colonies in the state; the Bureau of Indian Affairs estimates 65,000 ha of these on tribal lands (Cheyenne River Sioux Tribe, *in litt.).* These estimates suggest at least an 86% decline in prairie dog occupied area across the state.

lands and Wind Cave National Parks currently contain 1,660 and 3,085 ha of prairie dogs, respectively (NPS, *in litt.).* These numbers represent 2 and 4% respectively, of the area available on these public lands.

Texas

There were an estimated 31,385 ha of prairie dogs in northwest Texas in 1973 (Cheatham 1973). In 1991, there were at least 12,145 ha of prairie dogs estimated in Texas (Peggy Horner, Texas Parks and Wildlife, *in litt.).* Comparing this with a statewide historic estimate of 23,000,000 ha (Merriam 1902) results in a decline of over 99% in this century.

Wyoming

On Thunder Basin National Grassland, the Forest Service *(in litt.)* currently estimates 1,500 ha of active prairie dog colonies, with an additional 4,900 ha subject to periodic rodenticide treatment. Colony area for the period 1978 to 1980 was reported to be 2,550 ha (Schenbeck 1982). These numbers represent 0.6% of this 231,500 ha public grassland area. Devil's Tower National Monument contains approximately 16 ha of black-tailed prairie dogs (NPS, *in litt.);* 3% of the area available. Black-tailed prairie dogs in Wyoming may have increased in abundance near the turn of the century as a result of sheep and cattle grazing, with an estimated 53,650 ha by 1971 (Clark 1973). However, Campbell and Clark (1981) estimated a 75% reduction in prairie dog occupied areas since 1915. Current estimates indicate between 53,000 and 82,590 ha statewide (Wyoming Game and Fish Department, cited in FaunaWest Wildlife Consultants 1995).

SUMMARY OF PRAIRIE DOG STATUS IN EACH STATE

FaunaWest Wildlife Consultants (1995) attempted to estimate the amount of land area within the range of the black-tailed prairie dog that is currently occupied by the species. They included seven Great Plains states in their analysis and concluded that the states have less than a 1% occupancy of land surface within the species' range. The states included in this assessment and the percent of prairie dog occupancy within available area are Colorado (0.35%), Kansas (0.14%), Montana (0.17%), Nebraska (0.22%), North Dakota (0.17%), South Dakota (0.80%), and Wyoming (0.60 to 0.88%).

While these individual state accounts do not represent an exhaustive rangewide status review, they unfortunately provide the best information available. Significant reductions in occupied area have and continue to occur throughout the species' range; losses in some places exceeded 95%. Although the species still occurs in all but one state in its historic range, the eastern boundary of this distribution may be receding to the west. Figures indicate that there may be more than 550,000 ha of occupied black-tailed prairie dog range remaining in the United States, which is consistent with the estimate of 600,000 ha (Marsh 1984) cited previously. Over half the known prairie dog acreage in the central and northern Great Plains occurs on private land, almost 30% is on Indian reservations, and about 6% each occurs on Forest Service and Bureau of Land Management property (figure 2, FaunaWest Wildlife Consultants 1995). Neither Park Service nor Fish and Wildlife Service lands support significant acreage of any prairie dog species.

There is a need to develop a standardized survey technique for assessing prairie dog status. Presently, two methods are commonly employed and both involve mapping of individual prairie dog colonies either by ground reconnaissance or from aerial photo interpretation. Both methods are time consuming and expensive, making it unreasonable to expect a survey of over 500,000 ha of prairie dog colonies on the Great Plains within a short time period. Prairie dog colonies represent clumped patches on a broad landscape and there already exist nonmapping techniques that might be capable of statistical sampling of this distribution (Marcum and Loftsgaarden 1980). A statistical approach to monitoring prairie dog colony acreage may be a more appropriate technique than trying to map all prairie dog colonies.

PRAIRIE DOGS AND LIVESTOCK

Efforts to eradicate the prairie dog by the livestock and agricultural industry have existed for most of this century. Merriam (1902) estimated that prairie dogs caused a 50 to 75% reduction in range productivity. Taylor and Loftfield (1924) concluded that the prairie dog is"one of the most injurious rodents of the

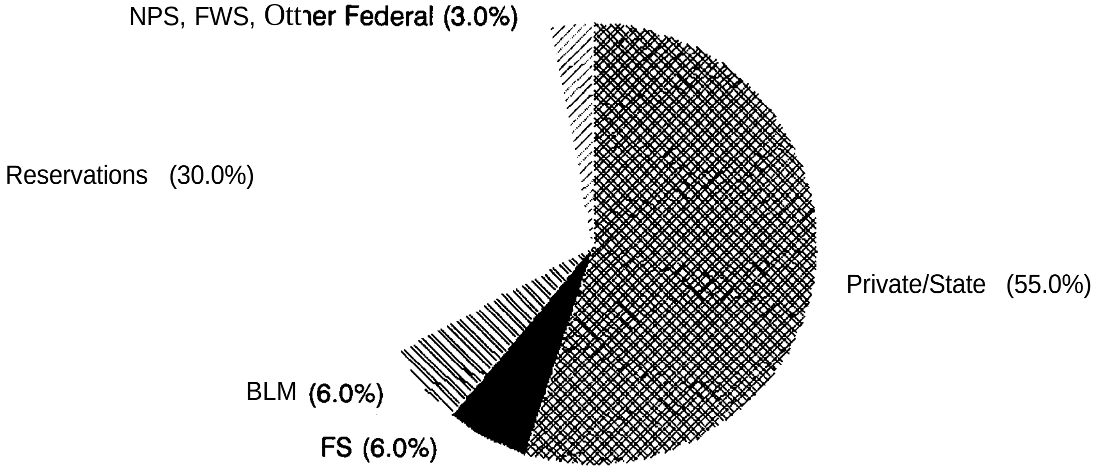

Figure 2. Distribution of black-tailed prairie dog colonies by land ownership in seven states in the northern and central Great Plains.

southwest and plains regions," and results in "the removal of vegetation in its entirety from the vicinity." Reports such as these were largely responsible for the escalating effort by range managers on the Great Plains to eradicate the prairie dog.

The conflict between the livestock industry and the prairie dog will likely not end easily or quickly, despite reports that prairie dog foraging does not significantly affect weight gain of cattle (O"Meilia et al. 1982; Hansen and Gold 1977). Others have reported the beneficial effects of prairie dogs on long-term range condition, including increased plant species diversity, richness, and overall plant production in prairie dog colonies (Archer et al. 1987; Uresk and Bjugstad 1983; Bonham and Lerwick 1976; Gold 1976). Uresk (1985) demonstrated that up to four years following prairie dog control, plant production was not increased whether the range was grazed or ungrazed by cattle.

Conversely, Hanson and Gold (1977) reported dietary overlap between cattle and prairie dogs, suggesting there may be some competition for the same species of forage plants. An estimation of true competition would be dependent on a variety of factors, including density of prairie dogs, stocking rate of cattle, ground cover, forage species present, and others (Uresk and Paulson 1988). Collins et al. (1984) reported that the annual cost of prairie dog poisoning was higher than the annual value of the forage gained by these measures. This issue requires more study, with input from both sides of the debate.

PRAIRIE DOGS AND BIODIVERSITY

The prairie dog, an integral component of the shortgrass prairie biotic community, is capable of transforming its own landscape and creating habitat alterations on a scale surpassed only by humans on the Great Plains. The ecosystem that is maintained by the prairie dog is valuable to many other species, with over 100 species of vertebrate wildlife reportedly using prairie dog colonies as habitat (Sharps and Uresk 1990; Clark et al. 1989; Reading et al. 1989). While few of these species are critically dependent on prairie dogs for all their life requisites, the increased biodiversity associated with prairie dog colonies indicates the importance of this habitat. Agnew et al. (1986) reported greater avian densities and species richness on prairie dog colonies. Also, numerous researchers have documented the preferential feeding of wild and domestic ungulates on prairie dog colonies (Coppock et al. 1983; Detling and 1987; Knowles 1986; Krueger 1986; Wydeven and Dahlgren 1985).

A number of rare and declining species are associated with prairie dogs and the habitat they provide. The black-footed ferret, *Mustela nigripes* Audubon and Bachman, 1851, is considered a true prairie dog obligate because it requires the prairie dog ecosystem for its survival. As one of the most endangered mammals in North America, this species has come to symbolize the decline in native grassland biodiversity. At least two species that are candidates for listing under the Endangered Species Act are also associated to a lesser degree with prairie dogs. The mountain plover, *Charadrius montanus* Townsend, 1837, and the swift fox, *Vulpes velox* Say, *1823,* are attracted to the vegetative changes and possibly increased food availability in prairie dog colonies. The association of other species that are either declining or vulnerable indicate the problems facing this habitat.

CONSERVATION EFFORTS

Prairie dogs are managed either directly or indirectly within the survey area by at least six federal agencies, 11 state wildlife departments, state agriculture departments, departments of state lands, and numerous weed and pest districts, counties and private landowners. Prairie dog management goals and objectives vary significantly among these entities. Even management within agencies but between areas varies significantly. This variation can range from total protection of prairie dogs to a legal mandate to exterminate. All states have simultaneously classified the prairie dog as a pest and as wildlife, often with opposing management goals. Federal policy regarding prairie dogs has been inconsistent over time and across geographic regions. The legal mechanisms responsible for the decline of prairie dogs during this century are still intact. Restoration of the prairie dog ecosystem may not be possible without major changes in management policy.

At least two federal agencies have taken the initiative to begin to address the problems associated with declining prairie dog occupied areas and to involve other interested parties. The Forest Service initiated a working group comprised of various federal land and resource agencies throughout the northern states in the Great Plains, involving the Bureau of Land Management, Park Service, Bureau of Indian Affairs, and Fish and Wildlife Service. The function of this group is to encourage development of conservation assessments and strategies for the species across broad landscapes.

In January 1995, the Fish and Wildlife Service convened a meeting of federal, state, and nongovernmental entities to discuss problems facing the shortgrass prairie ecosystem, including the prairie dog as a focal species. Consensus recommendations were: 1) Fish and Wildlife Service will develop conservation strategies to keep prairie species from becoming listed under the Endangered Species Act and to recover declining species before a listing occurs; and 2) work with the Western Governor's Association to investigate ways to coordinate and communicate with all involved parties on prairie issues. The Fish and Wildlife Service recognizes that prairie dog management remains within the jurisdiction of the various state and federal land management agencies. Therefore, this agency is particularly interested in participating in cooperative agreements with other agencies so that the prairie dog may be managed as a wildlife species rather than simply controlled as a pest.

CONCLUSION

The black-tailed prairie dog does not appear to be in danger of becoming extinct in the foreseeable future, given current management. However, the additional negative impacts resulting from habitat fragmentation (Wilcox and Murphy 1985) could seriously impact the ability of some prairie dog populations to persist or become re-established. Habitat fragmentation adversely quickly affects highly specialized species (Miller et al. 1994) and the myriad of species associated with prairie dog colonies recover from habitat or population losses at different rates. This could result in a significant disruption of the ecosystem overall functioning, further delaying its recovery. Such effects are already evident for the endangered black-footed ferret. The future recovery or extinction of this species is inextricably entwined with the decisions resource managers make today regarding the conservation of the prairie dog ecosystem.

Management of the black-tailed prairie dog must give greater consideration to developing an abundance and distribution of prairie dogs that will ensure long-term population persistence of associated species. As a minimum, we believe that broad areas of suitable grasslands should have from 1 to 3% of the area occupied by prairie dogs. Federally-owned lands should assume a greater share of this responsibility, with a goal of from 5 to 10% occupancy by prairie dogs. Maintaining this level of occupancy may allow resource managers to determine what actually constitutes a functioning prairie dog ecosystem, so attempts may be made to preserve this system into the future.

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LITERATURE CITED

Agnew, W.,D.W. Uresk, and R.M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent mixed-grass prairie in western South Dakota. J. Range Manage. 39:135-139.

Anderson, E., S.C. Forrest, T.W. Clark, and L. Richardson. 1986. Paleo-biology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* Audubon and Bachman (1851). Great Basin Naturalist Memoirs 8:11-62

Archer, S. M.G. Garrett, and J.K Detling. 1987. Rates of vegetation change associated with prairie dog grazing in North American mixed-grass prairie. Vegetatio 72:159-166

Bell, W.R. 1921. Death to the rodents. U.S. Dept. of Agric. Yearbook 1920:421-438.

Bonham, C.D. and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. J. Range Manage. 29:221-225.

Burnett, W.L. 1918. Rodents of Colorado in their economic relation. Office of State Entomology, Colorado Agric. Coll., Fort Collins, CO. Circ. 25:1-31.

Campbell, T.M. III. 1989. Prairie dog colony location surveys and black-footed ferret searches in Montana. Pages l-12 *in* T.W. Clark, D. Hinckley, and T. Rich, eds., The prairie dog ecosystem: managing for biological diversity. MT BLM Wildlife Technical Bull. No. 2.

Campbell, T.M. III and T.W. Clark. 1981. Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. Amer. Mid. Nat. 105:269-276.

Captive Breeding Specialist Group. 1992. Black-footed ferret recovery plan review, Washington, DC, 22-24 July. Captive Breeding Specialist Group, Apple Valley, MN. 43 pp.

Cheatham, L.K. 1973. Censusing prairie dog colonies using aerial photographs. Pages 77-88 *in* R.L. Linder and C.N. Hillman, eds. Black-footed ferret and prairie dog workshop. SD State Univ., Brookings, SD.

Clark, T.W. 1973. Prairie dogs and black-footed ferrets in Wyoming. Pages 88-101 *in* R.L. Linder and C.N. Hillman, eds. Black-footed ferret and prairie dog workshop. SD State Univ., Brookings, SD.

Clark, T.W. 1979. The hard life of the prairie dog. National Geographic 156(2):270-281.

Clark, T.W., D. Hinckley, and T. Rich, eds. 1989. The prairie dog ecosystem: managing for biological diversity. MT BLM Wildlife Technical Bull. No. 2.

Collins, A.R., J.P. Workman, and D.W. Uresk. 1984. An economic analysis of black-tailed prairie dog control. J. Range Manage. 37:358-361.

Coppock, D.L., J.K. Detling, J.E. Ellis, and M.I. Dyer. 1983. Plant herbivore interactions in a mixed grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1-9.

Cully, J.F., Jr. 1989. Plague in prairie dog ecosystems: importance for black-footed ferret management. In T.W. Clark, D. Hinckley, and T. Rich, eds., The prairie dog ecosystem: managing for biological diversity. MT BLM Wildlife Technical Bull. No. 2.

Detling, J.K. and A.D. Whicker. 1988. A control of ecosystem processes by prairie dogs and other grassland herbivores. Pages 23-29 *in* Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Rapid City, SD. U.S. Forest Service, Washington, DC.

Dinsmore, J.J. 1983. Mountain plover *(Charadrius montanus).* Pages 185-196 *in* Armbruster, J.S., ed. Impacts of coal surface mining on 25 migratory birds of high federal interest. U.S. Fish and Wildlife Service. FWS/OBS-83/35/

FaunaWest Wildlife Consultants. 1995. A summary of black-tailed prairie dog abundance and distribution on the central and northern Great Plains. Report prepared for Defenders of Wildlife, Missoula, MT. 46 pp. + app.

Flath, D.L. and T.W. Clark. 1986. Historic status of black-footed ferret habitat in Montana. Great Basin Nat. Mem. 8:63-71.

Fox, M. and C. Knowles. 1995. Economic and ecological evaluation of the Fort Belknap Indian Reservation fish and wildlife program. Poster presentation at MT Chapter of TWS, 31 Jan-l Feb, 1995, Billings, MT.

Gold, I.K. 1976. Effects of black-tailed prairie dog mounds on shortgrass vegetation. M.S. Thesis, CO State Univ., Fort Collins, CO. 39 pp.

Graul, W.D. 1980. Grassland management practices and bird communities. Pages 38-47 *in* DeGraff, R.M., Technical Coordinator. Management of western forests and grasslands for nongame birds. U.S. Forest Service. GTR INT-86.

Hall, E.R. and K.R. Kelson. 1959. The mammals of North America. Ronald Press, New York, NY.

Hanson, R. 1988. A Chronology of prairie dog control operations and related developments in South Dakota. Pages 121-122 *in* Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Rapid City, SD. U.S. Forest Service, Washington, DC.

Hanson, R.M. and I.K. Gold. 1977. Black-tailed prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. J. Range Manage. 30:210-214.

Hubbard, J.P. and C.G. Schmitt. 1984. The black-footed ferret in New Mexico. Endangered Species Program, Dept. of Game and Fish, Santa Fe, NM.

Knowles, C.J. 1986. Some relationships of black-tailed prairie dogs to livestockgrazing. Great Basin Nat. 46:198-203.

Knowles, C.J. and P.R. Knowles. 1994. A review of black-tailed prairie dog literature in relation to rangelands administered by the Custer National Forest. U.S. Forest Service. 61 pp.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecology 67:760-770.

Lantz, D.E. 1903. Destroying prairie dogs and pocket gophers. KS State Agric. College Bull. No. 116.

Lee, C.D. and R.F. Henderson. 1988. Kansas attitudes on prairie dog control. Pages 162-165 *in* Ninth Great Plains Wildlife Damage Control Workshop Proc.

Lock, R.A. 1973. Status of the black-footed ferret and black-tailed prairie dog in Nebraska. Pages 44-46 *in* R.L. Linder and C.N. Hillman, eds. Black-footed ferret and prairie dog workshop. SD State Univ., Brookings, SD.

Marcum, C.L. and D.O. Loftsgaarden. 1980. Anonmapping technique for studying habitat preferences. J. Wildl. Manage. 44:963-968.

Marsh, R.E. 1984. Ground squirrels, prairie dogs and marmots as pests on rangeland. Pages 195-208 *in* Proceedings of the conference for organization and practice of vertebrate pest control, Hampshire, England. Plant Protection Division, Fernherst, England.

Merriam, C.H. 1902. The prairie dog of the Great Plains. Pages 257-270 *in* Yearbook of the U.S. Dept. of Agric. 1901. U.S. Government Printing Office. Washington, DC.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8(3):677-681

O'Meilia, M.E., F.L. Knopf, and J.C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. J. Range Manage. 35:580-585.

Powell, K.L. and R.J. Robel. 1994. Size and location of black-tailed prairie dog towns in Meade and Gray Counties, Kansas. Trans. KS Acad. Sci. 97:44-49.

Reading, R.P., J.J. Grenston, S.R. Beissinger, and T.W. Clark. 1989. Attributes of black-tailed prairie dog colonies in north-central Montana, with management recommendations for the conservation of biodiversity. Pages 13-28 *in* T.W. Clark, D. Hinckley, and T. Rich, eds., The prairie dog ecosystem: managing for biological diversity. MT BLM Wildlife Technical Bull. No. 2.

Schenbeck, G.L. 1982. Management of black-tailed prairie dogs on the National Grasslands. Pages 207-217 in Fifth Great Plains Wildlife Damage Control Workshop Proc.

Seton, E.T. 1929. Lives of game animals. Doubleday, Dovan, and Co., Inc., Garden City, NY. 949 pp.

Shackford, J.S., J.D. Tyler, and L.L. Choate. 1990. A survey of the black-tailed prairie dog in Oklahoma. Final report submitted to OK Dept. of Wildlife Conservation. Cameron Univ., Lawton, OK. 18 pp.

Sharps, J.C. 1988. Politics, prairie dogs, and the sportsman. Pages 117-118 *in* Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Rapid City, SD. U.S. Forest Service, Washington, DC.

Sharps, J.C. and D.W. Uresk. 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. Great Basin Nat. 50:339-345.

Taylor, W.P. and J.V.G. Loftfield. 1924. Damage to range grasses by the Zuni prairie dog. U.S. Agric. Bull. 1227.

Tschetter, B.J. 1988. Estimates of South Dakota prairie dog acreages, 1987. Report No. 88.01. SD Dept. of Game, Fish and Parks, Pierre, SD.

U.S. General Accounting Office. 1988. More emphasis needed on declining and overstocked grazing allotments. GAO/RCED-88-80. Washington, DC.

Uresk, D.W. 1985. Effects of controlling black-tailed prairie dogs on plant production. J. Range Manage. 38:466-468.

Uresk, D.W. and A.J. Bjugstad. 1983. Prairie dogs as ecosystem regulators on the northern high plains. Pages 91-94 *in* Seventh North American Prairie Conference Proceedings, Southwest Missouri State Univ., Springfield, MO.

Uresk, D.W. and D.D. Paulson. 1988. Estimated carrying capacity for cattle competing with prairie dogs and forage utilization in western South Dakota. Pages 387-390 *in* Symposium on Management of Amphibians, Reptiles, and Small Mammals in North America. Flagstaff, AZ.

Vanderhoof, J.L., R.J. Robel, and K.E. Kemp. 1994. Numbers and extent of black-tailed prairie dog towns in Kansas. Trans. KS Acad. Sci. 97:36-43.

Wilcox, B.A. and D.D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. Amer. Nat. 125:879-887.

Wydeven, A.P. and R.B. Dahlgren. 1985. Ungulate habitat relationships in Wind Cave National Park. J. Wildl. Manage. 49:805-813.

The Role of Fire in Managing for Biological Diversity on Native Rangelands of the Northern Great Plains

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Abstract.-A strategy for using fire to manage for biological diversity on native rangelands in the Northern Great Plains incorporates an understanding of its past frequency, timing and intensity. Historically, lightning and humans were the major fire setters, and the role of fire varied both in space and time. A burning regime that includes fires at various intervals, seasons and intensities, including midsummer burns, should be reinstated. However, burning to enhance rare systems and species and to discourage exotic species is also needed. The goal is to base plans on an understanding of historic processes and ecosystem interactions, and resist techniques that rely on unexamined conventions.

INTRODUCTION

"A common thread runs through the many definitions of biological diversity: variety of life and its processes in a given area" (Salwasser 1990). A management strategy for conserving biological diversity of any natural ecosystem must focus on saving all the components, including the structure, composition (including genetic diversity), and processes that characterize these systems (Kaufmann et al. 1994). Biological diversity is more than just the identifiable parts; it also includes the symbioses and synergisms that make nature work (Salwasser 1990).

The importance of disturbances in shaping native communities has recently received more attention. Ecosystems are dynamic entities whose patterns and processes are shaped and sustained on the landscape by successional processes and by abiotic disturbances such as fire, drought, and wind. To sustain these ecosystems, processes that characterize the variability found in native ecosystems should be present and functioning, and management activities should conserve or restore historic disturbance patterns (Kaufmann et al. 1994). This paper describes a strategy for managing biological diversity of rangelands on the Northern Great Plains. The approach is based on restoring historical disturbance processes given the significantly altered landscape patterns of today. Plant nomenclature follows Great Plains Flora Association (1986) (table 1).

SETTING

The Northern Great Plains region includes North Dakota, South Dakota and Nebraska, plus the eastern portions of Montana and Wyoming, and extends northward into Manitoba, Saskatchewan and Alberta. The climate of the region is characterized by an increase in precipitation and humidity and a decrease in periodic droughts during the summer from west to east (Risser 1990). This climate range influences not only the potential native vegetation but also the fire regime and effects. The shortgrass prairie on the Western and Southern portions of the region is the most arid type; the mixed-grass prairie occurs in the midsection of the region; and the tallgrass prairie on the Eastern edge receives the most precipitation (Risser et al. 1981).

The variation in precipitation across the region greatly influences the growth and expansion of woody plants. In the most Western portion of the region, big sagebrush occupies uplands; in the absence of fire it persists or expands (Wright and Bailey 1982). In the remainder of the shortgrass and mixed-grass portions of the region, woody plants are restricted to areas of increased elevation, such as the Black Hills, or to areas of increased moisture such as riparian zones, draws, and north-facing slopes. Escarpments, ridges, and outcrops in the Western portion support rosa pine and Rocky Mountain juniper (Wells 1965).

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Table 1. Common and scientific names used in this report. Nomenclature follows GreatPlains Flora Association (1986).

Common name	Scientific name
Graminoids	
big bluestem	*Andropogon gerardii*
smooth brome	*Bromus inermis*
cheatgrass	*Bromus tectorum*
Japanese brome	*Bromus japonicus*
buffalo grass	*Buchloe dactyloides*
threadleaf sedge	*Carex filifolia*
sand dropseed	*Sporobolus cryptandrus*
green needlegrass	*Stipa viridula*
Forbs	
leafy spurge	*Euphorbia esula*
western prairie fringed orchid	*Platanthera praeclara*
Shrubs and trees	
sagebrush	*Artemisia* spp.
dwarf sagebrush	*Artemisia cana*
big sagebrush	*Artemisia tridentata*
green ash	*Fraxinus pennsylvanica*
Rocky Mountain juniper	*Juniperus scopulorum*
Eastern red cedar	*Juniperus virginianus*
cactus	*Opuntia* spp.
ponderosa pine	*Pinus ponderosa*
plains cottonwood	*Populus deltoides*
aspen	*Populus tremuloides*
chokecherry	*Prunus virginiana*
bur oak	*Quercus macrocarpa*
willows	*Salix* spp.
snowberry	*Symphoricarpos occidentalis*

Woody draws (narrow woodlands occurring in ravines) are examples of communities in more arid portions of the region that are restricted to sites with greater soil moisture. The most common woody plants in these draws are green ash and chokecherry. Riparian zones along streams and rivers support plains cottonwood, willows, and dwarf sagebrush (Severson and Boldt 1978). These woodlands may also expand in the absence of fire, but the expansion is restricted to sites with adequate moisture and the expansion rate is slower than in the tallgrass region. Further, many deciduous species, such as chokecherry and willows, sprout vigorously following burning (Wright and Bailey 1982). Only very frequent fires (i.e., every 1 to 5 years) would favor grasses over these species.

In contrast to more arid portions of the region, mesic prairies in the Northern, Eastern and Southeastern portions of the region are characterized by precipitation amounts high enough to support the expansion of woody plants onto uplands. It is in these areas that frequent fires slow the expansionof woody plants on uplands (Bragg and Hulbert 1976). In the Northern portion of the region, aspen replaces ponderosa pine on outcrops and expands into the Canadian prairies (Wright and Bailey 1982). Eastern red cedar replaces Rocky Mountain juniper in the Southeastern part of the region where it readily expands onto uplands (Gehring and Bragg 1992). In the eastern tallgrass prairies, woody species, such as willows and bur oak, invade grasslands, and only frequent fires slow their expansion (Anderson 1990). Plains cottonwood and willow dominate floodplains in the more mesic portions of the Northern Great Plains; green ash and bur oak are common on higher terraces along major rivers (Johnson et al. 1976).

In addition to climatic factors, herbivores also influence the region's vegetation and fire regimes. However, it is difficult to distinguish the particular influence each force has on vegetation (Henderson and Statz 1995). Fire is often associated with periodic drought, and fire and grazing are sometimes interrelated. For example, recently burned grasslands often attract grazers; yet, heavily grazed areas usually resist fire until dead litter reaccumulates (Steuter et al. 1990, Vinton et al. 1993). Therefore, the influences of grazing and drought must be a part of a discussion of historical fire effects (Henderson and Statz 1995).

FIRE HISTORY

An understanding of the frequency, timing, and intensities of past fires is necessary before fire can be incorporated into a strategy to conserve prairie systems. Based on data from adjoining ponderosa pine forests, which indicated that fire frequency varied from 2 to 25 years, Wright and Bailey (1982) estimate that on level-to-rolling topography, a fire frequency of 5 to 10 years in the Northern Great Plains is reasonable. On topography more dissected with breaks and rivers, they estimate a fire frequency of 20 to 30 years. Wendtland and Dodd (1992) agree with this range, based on their examination of historical documents and fire records from the Scotts Bluff National Monument area in northwestern Nebraska. Dendrochronology data in the Devils Tower region northwest of the Black Hills reveal that before 1770 the mean interval between fires was 27 years; from 1770 to the fire return interval was 14 years (Fisher et al. 1987). Brown and Sieg (1996) report a mean fire frequency in the south-central Black Hills of 16 years for the period 1388 to 1918.

In the more mesic portions of the Northern Great Plains, the average fire return interval was shorter. Collins and Gibson (1990) estimate a frequency of every 1 to 5 years in the tallgrass portions of this region. In northcentral Nebraska, the fire return interval averaged 3.5 years between 1851 and 1900 (Bragg 1985).

Historically, the major ignition sources for prairie fires were lightning and American Indians. Lightning was, and is, an important ignition source in the Northern Great Plains. In northwestern South Dakota, lightning-set fires occur an average of 6 to 25 times per year, and most commonly occur in July and August (Higgins 1984); fewer occur in April, May, June, and September. Wendtland and Dodd (1992) note that of 10 fires described in historical documents between 1824 and 1934, and of 26 fires officially recorded between 1934 and 1969 in the Scotts Bluff National Monument area, over 70 percent occurred in July and August.

Higgins' (1986) review of 300 historical accounts written between 1673 and 1920 reveals that fires accidentally or intentionally set by American Indians were common in the Northern Great Plains. He found that although Indians set fires in nearly every month of the year, April, September and October were their peak fire-setting times. The majority of the 97 fires described were scattered, single events of short duration and small extent; only 10 fires burned longer than 1 day.

American Indians had many uses for fire. These included attracting and herding wild animals, signaling threats and warnings, improving pasturage, masking and eliminating personal signs at camps and along trails, and for pleasure, warfare and ceremonies (Higgins 1986). During their 10,000-year occupation of this region, the timing of fires set by American Indians did not mirror lightning-set fires; therefore, these Indian-set fires can be considered additive to lightning fires (Higgins 1986).

A combination of periodic droughts, high temperatures and strong winds in the region provide the components necessary for fire spread (Collins 1990). The end result of the erratic climate, flammable fuels, topographic relief and other factors, such as grazing animals, was that the role of fire was not constant in time or space (Anderson 1990).

With the arrival of non-native settlers came fire suppression policies and, in many areas, a shift in the timing of fires. Near Devils Tower, Wyoming, after 1900, the fire return interval increased to every 42 years, versus less than every 27 years previously (Fisher et al. 1987). In the south-central Black Hills, Brown and Sieg (1996) record a 104-year fire-free period in ponderosa pine stands between 1890 and 1994, and note that most of past fires occurred late in the growing season or after growth had ceased for the year. Higgins (1984) suggests that the recent extent and spread of lightning fires has been modified by cultural features such as roads; further, the fire regime has also been altered by differing patterns of grazing animals (first bison, then cattle). In contrast to the late summer ignitions that commonly burned before 1935 near Scotts Bluff, Nebraska, the 46 fires recorded since 1935 dramatically shifted to spring occurrences (Wendtland and Dodd 1992). Lengthening the interval between fires, shifting from summer to early spring burning, and/or reducing fire intensity by prescribing cooler fires may alter species composition to favor fire-intolerant species (Wendtland and Dodd 1992) such as cactus and non-sprouting woody species like sagebrush (Wright and Bailey 1982).

DEVELOPING A FIRE MANAGEMENT STRATEGY TO CONSERVE DIVERSITY

The fire strategy most likely to manage diversity on native rangelands of the Northern Great Plains is based on two premises: 1) processes that mimic, as much as possible, the variability found in native ecosystems should be present and functioning; and 2) management activities should conserve or restore historical disturbance patterns (Kaufmann et al. 1994). This management strategy should reflect the differing roles that fire historically played in the various portions of the region. However, this strategy must also address the fundamental changes that have occurred in the landscape such as drastically different landscape patterns imposed by species changes and management unit boundaries.

Wendtland and Dodd (1992) recommend a scenario that mimics the presettlement fire history. For the Scotts Bluff, Nebraska area, they infer this strategy including high intensity summer fires on a return interval of 5 to 30 years. Shifting burning programs from all spring or fall burns to include some midsummer burns should favor some species not enhanced by spring or fall burns (Howe 1994). For example, an April fire burns early foliage critical for root production of cool-season plants, leaving late-season plants unscathed; an August fire burns the largely inactive foliage of cool-season species, while consuming foliage and reproductive stems of warm-season species (Howe 1994). However, historically, fires occurring after fuels have cured in the fall or in the early spring before green-up may have been more significant than summer fires. High fuel moisture in July and August and concurrent slow rates of spread result in a smaller area being burned by an individual fire, compared to those fires occurring when fuels are cured in the fall (Steuter 1988). Given the highly variable fire regime in the past, burns of varying intensities at differing seasons are appropriate. Further, the interval between fires should be varied to best restore fire disturbance patterns of the Northern Great Plains. The strategy should avoid a uniformity in timing of burns or in intervals between burns that artificially simplifies what was probably a more complex system (Howe 1994).

SPECIAL HABITATS AND SENSITIVE SPECIES

Reinstituting a fire regime based on historical processes that includes burning at varying intervals and in differing seasons is the first step in developing a strategy for using fire to manage biological diversity on native rangelands in this region. The second step involves assessing the direct and indirect impacts of fire on special habitats and sensitive species. Special habitats are native biological communities or ecosystems that are rare, unique, or highly productive elements of regional landscapes (Salwasser 1990). Sensitive species include those native species currently in danger of extinction or those whose population trends are negatively affected by human actions (Salwasser 1990). The burning strategy should also consider the potentially different historical fire disturbance regimes in these sensitive ecosystems, minimize potential negative influences of fire, and maximize conditions favorable to the expansion of these systems and species.

The special habitats in the Northern Great Plains (wetlands, lowlands, and riparian areas) contain high numbers of listed vulnerable species (Finch 1992, Finch and Ruggiero 1993). Although each of these habitats constitutes a relatively small percentage of the total land area, each contributes disproportionately to the diversity of native rangelands in this region (Finch and Ruggiero 1993). If sensitive communities such as these occur within a management unit, burning programs should be examined relative to their impacts on these habitats. The range in frequency, timing, and intensity of burns suitable to upland habitats may not provide optimum conditions for sustaining these distinctive systems.

Wetlands, lowlands, and riparian woodlands in this region are examples of communities that, because of higher moisture, likely burned less frequently than uplands. Riparian zones throughout the region, and woody draws in the more arid portions, tend to be green throughout most of the growing season, have higher relative humidities than adjacent grasslands, and often have running water or moist soils that slow the spread of fire into these communities. In most years, prairie fires would skip over or only burn lightly through these narrow woodlands (Severson and Boldt 1978). However, the narrow configuration and close contact of these woodlands with flammable grassland fuels suggest that historically they were exposed to a high number of grassland fires. Fire inevitably entered these woodlands, especially in dry years on hot and windy days.

Given that the species composition in woody draws includes a number of deciduous species, such as snowberry and chokecherry, that sprout following burning (Wright and Bailey 1982), and that several woody species establish best in mineral soils, fire probably functioned as a regeneration mechanism in these systems. Further, since these communities stay green longer than uplands, fires probably burned late in the growing season when there were adequate levels of cured, fine fuel. Repeated, annual fires, especially during droughts, tend to favor the growth of grasses over woody plants (Wright and Bailey 1982). Fires occurring infrequently when plants dormant, followed by high precipitation, may enhance woody plant growth (Wright and Bailey 1982, Sieg 1991). If the goal is to regenerate woody plants in woody draws and/or to mimic historical fires, prescriptions should be set to achieve high intensities (Sieg 1996).

Rocky Mountain juniper woodlands are an example of a relatively uncommon community in the Western portion of the Northern Great Plains that rarely burned. In this region, Rocky Mountain juniper grows best on steep barren slopes (Noble 1990) where the sparse understory vegetation is rarely adequate to sustain a fire. In areas where fine fuels are sufficient to carry a fire, the high volatile oil content of the foliage combined with Rocky Mountain juniper's inability to sprout following topkilling, results in high mortality rates (Wright and Bailey 1982).

Threatened or endangered species are examples of sensitive species whose needs cannot be ignored. Because they are the first species to drop out of ecosystems, they are considered the weakest link in the conservation of native biological diversity (Finch and Ruggiero 1993). Providing habitats in an appropriate spatial and temporal arrangement is necessary to maintain viable populations of sensitive species. Thus, vegetation management is a major tool for maintaining and restoring biodiversity, and for delisting or avoiding listing of threatened and endangered species (Kaufmann et al. 1994).

Adjusting fire management programs to meet the needs of threatened and endangered species requires an understanding of the role of fire in the long-term sustainability of the ecosystems supporting these species, and in the life history and habitat needs of individual species. For example, the western prairie fringed orchid is a federally listed threatened plant species associated with swales (low-lying often wet land) of the tallgrass prairie (U.S. Fish and Wildlife Service 1989). Although the tallgrass prairie is prone to burn every 1 to 5 years (Collins and Gibson 1990), it is unlikely that swales supporting orchids burned as often, especially during years when they were flooded. Vogl(l969) describes a "quasi-equilibrium" of a Wisconsin lowland maintained by floods during wet periods and fires during droughts. Lowlands supporting orchid populations likely burned throughout the growing season during prolonged droughts; however, fires that occur when orchids are actively growing are apt to injure or kill them. Since fall burning allows orchids to complete their life cycle, and dry conditions and lightning are inclined to occur late in the growing season, fall fires are a better choice than spring burning to sustain orchid populations and their associated habitat (Bjugstad-Porter 1993).

MANAGE INTRODUCED SPECIES

The introduction of exotic species to new environments without their associated parasites and pests may be humankind's greatest environmental manipulation (Young and Evans 1976). Many invasive exotic species have characteristics that enable them to vigorously compete with native plants and to exploit disturbed areas (Parker et al. 1993). In addition to reviewing impacts of existing non-native species and preventing the introduction of new ones (Kaufmann et al. 1994), management plans should address how to manage these species; fire is a useful tool in this arena. Problem species include those purposely planted, such as smooth brome, and a variety of species accidentally introduced, such as cheatgrass, Japanese brome, and leafy spurge (Lym 1991).

Although burning is not a panacea for discouraging introduced species, with careful planning it can be a useful tool, especially if native species are not adversely affected. Burning at a time when plants are most vulnerable is useful for suppressing undesirable species. For example, burning in mid-or late May, when smooth brome tillers are either elongating or heading, reduces tiller density of smooth brome by 50 percent when compared to unburned plots in Nebraska (Willson 1992). Burning in May also enhances production of flowering culms of some native warm-season grasses such as big bluestem (Willson 1992). However, burning is not a cure-all for reducing persistent species such as smooth brome, and the outcome is strongly dependent on other factors such as climate and precipitation patterns. Subsequent burning in Pipestone, Minnesota failed to significantly reduce smooth tiller density (Willson and Stubbendieck 1996).

In addition to killing or injuring individual exotic plants, burning can be used to make the habitat less conducive to a species expansion. Spring burning in western South Dakota killed Japanese brome seedlings for one growing season, and by reducing litter accumulations, decreased future germination rates (Whisenant and Uresk 1990). In this case, spring burning was detrimental to the production of one native species, green needlegrass; enhanced production of two others, buffalo grass and sand dropseed; and did not change the production of a fourth, threadleaf sedge (Whisenant and Uresk 1990).

A combination of burning and other management tools may be valuable in managing invasive species. For example, picloram plus 2,4-D applied in the fall followed by spring burning reduced the stem density and germination rates of leafy spurge in North Dakota more than any other treatment tested (Wolters et al. 1994). The key to success in managing invasive species is to begin treatment before sive spread occurs and to focus as much as possible on the invaded ecosystem rather than on the invader (Hobbs and Humphries 1995).

SUMMARY

A strategy for using fire to manage native biological diversity on rangelands in the Northern Great Plains should consider natural disturbance patterns. Fires historically occurred as often as every 1 to 5 years in the more mesic portions of the region, but less frequently in areas of rough topography and in lowlands. Lightning, a major ignition source in this region, caused fires most often in July and August. American Indians accidentally or intentionally set fires in nearly every month of the year; however, the greatest number were set in April, September, and October. The end result of the erratic climate, fuels, topographic relief and factors such as grazing animals, was that the role of fire was not constant in time or space.

Reinstituting a fire regime based on historical processes, including burning at varying intervals (to reflect climatic patterns) and in differing seasons, is the first step in developing a strategy for using fire to manage for biological diversity on native rangelands in this region. Including mid-summer burns, rather than concentrating all prescribed burning in the spring and fall, would better mimic natural disturbance patterns. The second step involves adjusting fire regimes to best sustain special habitats, such as wetlands and riparian zones, and sensitive species, especially threatened and endangered ones. Third, fire prescriptions should be planned so that burning does not enhance the spread of invasive species. The overall goal is to base the fire management strategy on an understanding of historic processes and ecosystem interactions, and resist techniques that rely on unexamined conventions (Howe 1994).

ACKNOWLEDGMENTS

Dr. Kenneth F. Higgins, National Biological Service, South Dakota Cooperative Unit, Brookings; Dr. Allen Steuter, The Nature Conservancy, Niobrara Valley Preserve, Johnstown, NE; and Kate Cannon, Superintendent, Jewel Cave National Monument, Custer, SD provided comments helpful in revising an earlier draft of this paper.

LITERATURE CITED

Anderson, Roger C. 1990. The historic role of fire in the North American grassland. In: Fire in North American Tallgrass Prairies. Collins, Scott L; Wallace, Linda L., eds. Norman, OK: Univ. Oklahoma Press. 8-18.

Bjugstad-Porter, Rochelle. 1993. The western prairie fringed orchid *(Platanthera praeclara):* it’s response to burning and associated mycorrhizal fungi. Laramie, WY: University of Wyoming. 116 p. M.S. thesis.

Bragg, Thomas B. 1985. A preliminary fire history of the oak/pine forest of northcentral Nebraska. In: Proc. 95th Ann. Meet. Nebr. Acad. Sci., Lincoln, NE: Nebraska Wesleyan University. 8.

Bragg, Thomas B.; Hulbert, Lloyd C. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management. 29:19-24.

Brown, Peter M. and Carolyn Hull Sieg. 1996. Fire history in interior ponderosa pine communities of the Black Hills, South Dakota. International Journal of Wildland Fire. 6:97-105.

Collins, Scott L. 1990. Introduction: fire as a natural disturbance in tallgrass prairie ecosystems. In: Fire in North American Tallgrass Prairies. Collins, Scott L; Wallace, Linda L., eds. Norman, OK: Univ. Oklahoma Press. 3-7.

Collins, Scott L.; Gibson, David J. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. In: Fire in North American Tallgrass Prairies. Collins, Scott L; Wallace, Linda L., eds. Norman, OK: Univ. Oklahoma Press. 81-98.

Finch, D.M. 1992. Threatened, endangered, and vulnerable species of terrestrial vertebrates in the Rocky Mountain Region. Gen. Tech. Rep. RM-215. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 38 pp.

Finch, Deborah M.; Ruggiero, Leonard F. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and Northern Great Plains. Natural Areas Journal. 13:191-203.

Fisher, R.F.; Jenkins, M.J.; Fischer, William F. 1987. Fire and the prairie-forest mosaic of Devils Tower National Monument. American Midland Naturalist. 117:250-257.

Gehring, Janet L; Bragg, Thomas B. 1992. Changes in prairie vegetation under eastern red cedar (Juniperus *virginiana* L.) in an eastern Nebraska bluestem prairie. American Midland Naturalist

Great Plains Flora Association. 1986. Flora of the Great Plains. Lawrence, KS: Univ. Press of Kansas. 1392 pp.

Henderson, Richard A.; Statz, Sandra H. 1995. Bibliography of fire effects and related literature applicable to the ecosystems and species of Wisconsin. Technical Bulletin No. 187, Department of Natural Resources, Madison. 56 pp.

Higgins, Kenneth F. 1984. Lightning fires in North Dakota grasslands and in pine-savanna lands of South Dakota and Montana. Journal of Range Management. 37:100-103.

Higgins, Kenneth F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. Res. Pub. 161. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. 39 pp.

Hobbs, Richard J.; Humphries, Stella E. 1995. An integrated approach to the ecology and management of plant invasions. Conservation Biology. 9:761-770.

Howe, Henry F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology. 8:691-704.

Johnson, W. Carter; Burgess, Robert L.; Keammerer, Warren R. 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. Ecological Monograph. 46:59-84.

Kaufmann, Merrill R.; Graham, Russell T.; Boyce, Douglas A., Jr. [et al.]. 1994. An ecological basis for ecosystem management. Gen. Tech. Rep. RM-246. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 22 pp.

Lym, Rodney G. 1991. Economic impact, classification, distribution, and ecology of leafy spurge. In: Noxious Range Weeds. James, Lynn F.; Evans, John 0.; Ralphs, Michael H.; Child, R. Dennis, eds. Boulder, CO: Westview Press. 169-181.

Noble, Daniel L. 1990. *Juniperus scopulorum* Sarg. Rocky Mountain juniper. In: Silvics of North America, Vol. 1. Agric. Handb. 654. Burns, Russell M.; Honkala, Barbara H., Tech. Coords. Washington, DC: U.S. Department of Agriculture, Forest Service. 116-126.

Parker, Ingrid M.; Mertens, Shoshana K.; Schemske, Douglas W. 1993. Distribution of seven native and two exotic plants in a tallgrass prairie in southeastern Wisconsin: the importance of human disturbance. American Midland Naturalist. 130:43-55.

Risser, Paul G. 1990. Landscape processes and the vegetation of the North American grassland. In: Fire in North American Tallgrass Prairies. Collins, Scott L; Wallace, Linda L., eds. Norman, OK: Univ. Oklahoma Press. 133-146.

Risser, P.G.; Birney, E.C.; Blocker, H.D. [et al.]. 1981. The true prairie ecosystem. Stroudsburg, PA: Hutchinson Ross.

Salwasser, Hal. 1990. Conserving biological diversity: a perspective on scope and approaches. Forest Ecology and Management. 35:79-90.

Severson, Kieth E.; Boldt, Charles E. 1978. Cattle, wildlife, and riparian habitats in the western Dakotas. In: Management and use of Northern Plains rangeland Regional Rangeland Symposium; 1978 Feb. 27-28; Bismarck, ND: North Dakota State University. 91-103.

Sieg, Carolyn Hull. 1991. Ecology of bur oak woodlands in the foothills of the Black Hills, South Dakota. Lubbock, TX: Texas Tech University. 185 p. Ph.D. Thesis.

Sieg, Carolyn Hull. 1996. The role of prescribed burning in regenerating *Quercus macrocarpa* and associated woody plants in stringer woodlands in the Black Hills, South Dakota. International Journal of Wildland Fire. 6:21-29.

Steuter, A.A. 1988. Restoring a mixed prairie process: the fire-bison grazing interaction. Bulletin of the Ecological Society of America. 69:308.

Steuter, Allen A.; Grygiel, C.E.; Biondini, M.E. 1990. A synthesis approach to research and management planning: the conceptual development and implementation. Natural Areas Journal. 10:61-68.

U.S. Fish and Wildlife Service. 1989. Endangered and threatened wildlife and plants; determination of threatened status for *Platanthera leucophaea* (eastern prairie fringed orchid) and *Platanthera praeclara* (western prairie fringed orchid). Federal Register 54:39857-39862.

Vinton, Mary Ann; Hartnett, David C.; Finck, Elmer J.; Briggs, John M. 1993. Interactive effects of fire, bison (Bison *bison)* grazing and plant community composition in tallgrass prairie. American Midland Naturalist. 129:10-18.

Vogl, Richard J. 1969. One hundred and thirty years of plant succession in a southeastern Wisconsin lowland. Ecology. 50-248-255.

Wells, Philip V. 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains region. Science. 148:246-249.

Wendtland, Kyle J.; Dodd, Jerrold L. 1992. The fire history of Scotts Bluff National Monument. In: Proceedings of the 12th North American Prairie Conference; Smith, Daryl D.; Jacobs, Carol A., eds. 1990, August 5-9; Cedar Falls, IA: University of Northern Iowa. 141-143.

Whisenant, Steven G; Uresk, Daniel W. 1990. Spring burning Japanese brome in a western wheatgrass community. Journal of Range Management. 43:205-208.

Willson, Gary D. 1992. Morphological characteristics of smooth brome used to determine a prescribed burn date. In: Proceedings of the 12th North American Prairie Conference; Smith, Daryl D.; Jacobs, Carol A., eds. 1990, August 5-9; Cedar Falls, IA: University of Northern Iowa. 113-116.

Willson, Gary D.; Stubbendieck, James. 1996. Suppression of smooth brome by Atrazine, mowing and fire. The Prairie Naturalist.

Wolters, Gale L.; Sieg, Carolyn Hull; Bjugstad, Ardell J.; Gartner, F. Robert. 1994. Herbicide and fire effects on leafy spurge density and seed germination. Res. Note RM-526. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 5 pp.

Wright, Henry A.; Bailey, Arthur W. 1982. Fire Ecology. New York: John Wiley & Sons. 501 pp.

Young, James A.; Evans, Raymond A. 1976. Responses of weed populations to human manipulations of the natural environment. Weed Science. 24:186-190.

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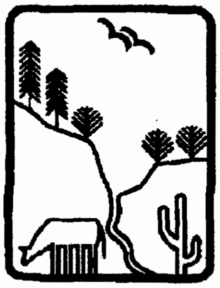
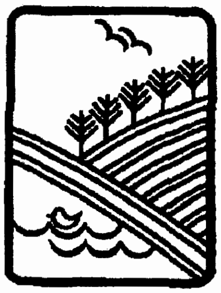
Rocky Mountain Forest and Range Experiment Station

Rocky Mountains



Southwest



Great Plains

The Rocky Mountain Station is one of seven regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota

*Station Headquarters: 240 W. Prospect Rd., Fort Collins, CO 80526

COMPLETED PRAIRIE DOG MANAGEMENT ON THUNDER BASIN NATIONAL GRASSLAND

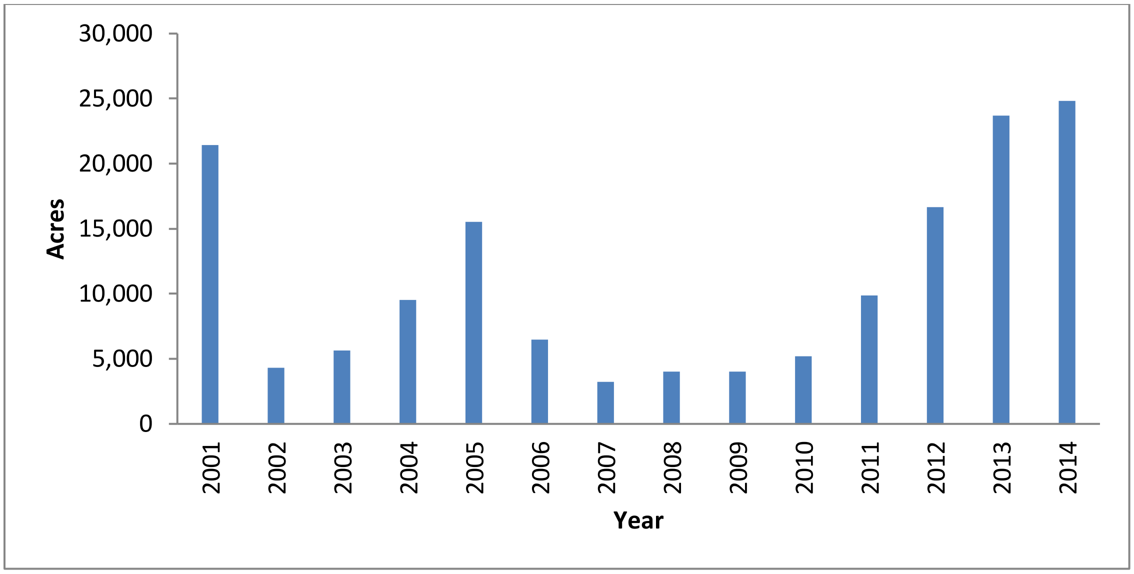
2014

The Land and Resource Management Plan (Grassland Plan) for the Thunder Basin National Grassland, Wyoming was amended in 2009 to better provide for the conservation of black-tailed prairie dogs and their habitat, to address private landowner concerns about unwanted prairie dog encroachment onto private lands within and adjacent to the TBNG boundaries, and to facilitate future recovery of endangered black-footed ferrets. Implementation has included:

- Prescribed burning
- Mowing
- Temporary fence
- Permanent vegetative buffer fence
- Dusting
- Larger shooting closure
- No shooting portal signs installed
- Translocation
- Rodenticide application
- Raptor perch construction

MAPPING

All active prairie dog colonies on Thunder Basin NG are mapped annually. Currently, the population for 2014 is **24,824** acres. The current acreage of occupied prairie dog colonies is approximately **4.5%** of the Thunder Basin NG.



Acres by Category:

Category	Acres	Objective	Current % of Objective
1	15,508	18,000	86%
2	1,411	3,000	47%
3	2,776	1,000	277%
4	1,592	4,000	39%
Control	3,231	NA	
New	306	NA	

POTENTIAL HABITAT MODELING

In an effort to help determine future prairie dog expansion, the entire TBNG was modeled using existing GIS layers that contained information related to slope, soil, and satellite imagery to determine vegetation cover. Using this information to exclude non-habitat, the remaining possible habitat was then field verified to determine if it was potential prairie dog habitat. Approximately 128,283 acres (NFS) are considered potential habitat using the variables available for the modeling. This is approximately 23% of the entire TBNG. Of that 128, 283 acres, 86,318 are strictly 'Potential' (i.e. have not been occupied by PDogs according to our data, but are capable of supporting habitat), 24,727 are Suitable Occupied (i.e. occupied in 2014) and 17,238 are Suitable Historically Occupied (i.e. not occupied in 2014 but occupied previously at some other time). A Habitat Suitability Index Model has not been completed, due to the lack of more specific available variables.

BURNING

Prescribed fire and grazing were identified in the TBGA AMP EIS as a tool that could be used to achieve desired conditions for vegetative resources. The purpose of burning is to provide diverse and quality grassland habitat across the geographic area at levels that, in combination with habitat on adjoining lands, helps support stable or increasing populations of plover and prairie dogs and other wildlife with similar habitat needs. Burning was a tool identified to move vegetation resources toward desired conditions, benefiting wildlife habitat. Guidelines in the LRMP direct management to schedule prescribed fire activities at intervals designed to improve or maintain habitats of desired plant and animal species.

Due to an unstable political climate surrounding prairie dog management on Thunder Basin NG, prescribed burning has been precluded as an implementation tool since 2012.

Acres completed:

- 2009 – 2,193 acres
- 2010 – 2,500 acres
- 2011 – 4,000 acres
- 2012 – 2,500 acres

TRANSLOCATION

Translocation is a tool identified to provide for the conservation of black-tailed prairie dogs and their habitat, and to address private landowner concerns about unwanted prairie dog encroachment onto private lands within and adjacent to the TBNG boundaries.

As with prescribed fire, due to an unstable political climate surrounding prairie dog management on Thunder Basin NG, translocation has been precluded as an implementation tool since 2011.

Acres Completed/Number of Prairie Dogs Moved:

- 2010 – 550 prairie dogs (120 acres)
- 2011 – 349 prairie dogs (166 acres)

MOWING

Mowing was completed for translocation preparation to encourage prairie dogs to stay where they have been moved to. This is a tool that up until now has only been used as preparation for translocation, but it has potential to be used in the same way as prescribed fire is to reduce grass height to encourage prairie dog colony expansion, or discourage expansion onto private lands.

- 2010 – 12 acres
- 2011 – 40 acres

DUSTING

We applied Delta Dust to prevent plague transmission across Grassland, and to colonies within 1 mile of residences that have expressed concerns. It is worth noting that all of the Delta Dust for 2012 was either donated by the Bayer Corporation or purchased by WWF. In 2013, all dust was donated by WWF, PDC, and Defenders. They also exclusively paid for the WCC crews that did the majority of the dusting. The FS provided oversight and additional ground support while crews were here.

Acres Completed:

- 2010 – 132 acres
- 2011 – 1,997 acres
- 2012 – 780 acres
- 2013 – 3,000 acres
- 2014 – 2,400 acres

Burrow Density Data from Dusting:

- 2012 – 33 burrows/acre
- 2013 – 21 burrows/acre
- 2014 – 35 burrows/acre

SIGNING

We constructed wood portal type signs at every major road entrance into shooting closure to inform public of where the shooting closure was located. We also installed carsonites on two-tracks that enter the shooting closure area, and 3.63. We will continue to install signs as funding allows.

Signs Installed:

- 2010 – 4 signs
- 2011 – 8 wooden portal signs, 30 carsonite signs.

BUFFER FENCE CONSTRUCTION

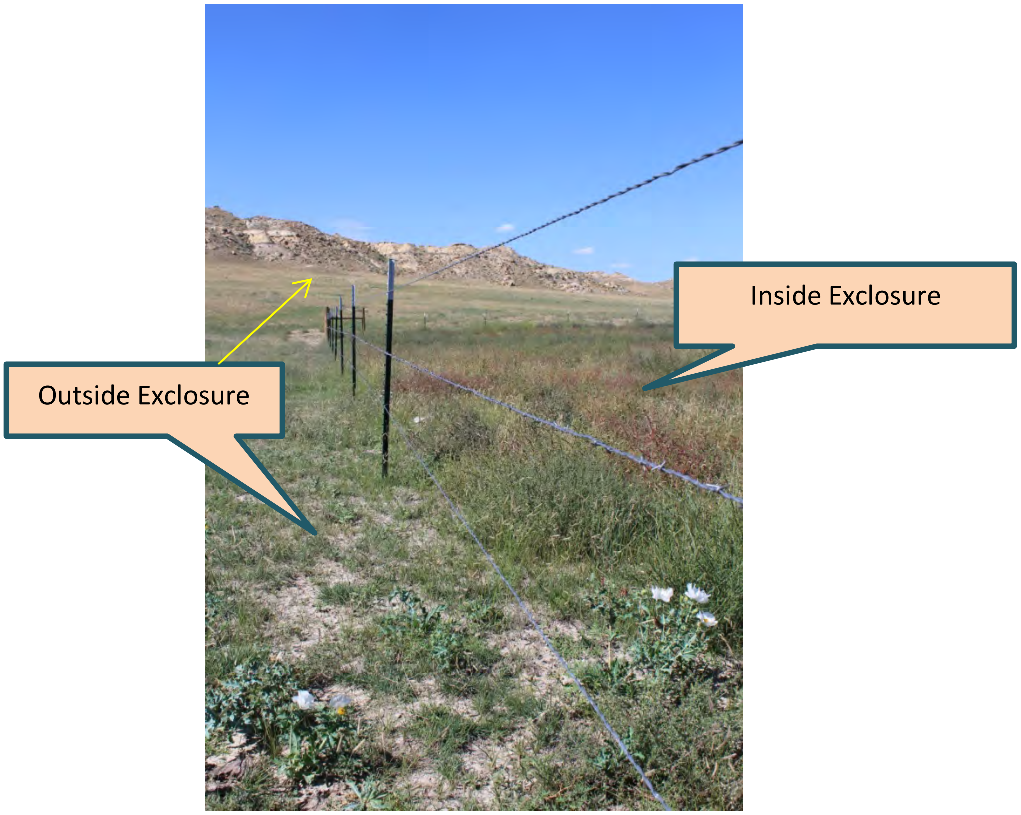
Constructed approximately 150 acres of permanent fence in 2010 around trapping site to create a vegetative buffer and prevent future re-colonization by prairie dogs. The Wyoming State Forestry Honor Farm built the majority of the fence at no cost to the USFS.

Acres Fenced:

- 2010 – 150 acres

2014 Conditions:

Based on 2014 monitoring, it appears that the remaining exclosure has been successful at reducing re-colonization following translocation and rodenticide use. There is only one small area within the exclosure that currently has prairie dogs, and this area is right next to the fence against private land. The private land located next to the FS exclosure continues to be heavily grazed by cattle, and includes installation of water and minerals stations. The private landowner has been unsuccessful at reducing the population of prairie dogs on the private land next to FS land, which are migrating onto the FS land within the exclosure. (all pictures were taken on FS land). Poisoning of prairie dogs currently occupying the NE side of the exlcousre will occur in October of 2014.


Inside Exclosure
Outside Exclosure


Inside Exclosure
Outside Exclosure

BUFFER FENCE REMOVAL

In 2012, in response to a complaint by 4W ranch, we removed 1 of the 2 buffer fences constructed in 2010. This was the most northern exclosure and it was 66 acres in size. All fence material was removed with assistance from the WCC crew, and donated to the range shop to use in fence repair/restoration from fire loss.

Acres Removed:

- 2012 – 66 acres

2013 Conditions:

Due to the removal of the buffer fence and lack of prairie dog control on adjacent private lands, prairie dogs have re-colonized the area that has been translocated once and poisoned three times. With lack of control on the private land, and no type of barrier to minimize re-colonization, the area appears to be back to pre-translocation numbers.

RODENTICIDE APPLICATION

Completed to address the issue of human health and safety concerns, and expansion on to private land as identified in the strategy. The acres listed with 2014 are expected to be completed in October of 2014.

Acres Poisoned:

- 2010 – 100 acres
- 2011 – 536 acres
- 2012 – 1,157 acres
- 2013 – 2,105 acres
- 2014 – 1,200 acres

SHOOTING CLOSURE EXPANSION

2010 - Expands shooting closure from 72,500 acres to 100,460 acres.

RAPTOR PERCHES

We constructed raptor perches to help encourage natural predation on prairie dog colonies that were along private land boundaries to help provide some control.

Perches Installed:

- 2011 – 2 perches

VEGETATION MONITORING

Monitoring of vegetation within sites impacted by prairie dogs was started in 2011 to determine what these impacts were, and how potentially they could affect forage to livestock. Currently, the FS is working with Dr. Jack Butler to design and implement more vegetation monitoring, and to potentially enlist him to do a 2-3 year research project on TBNG.

Sites Monitored:

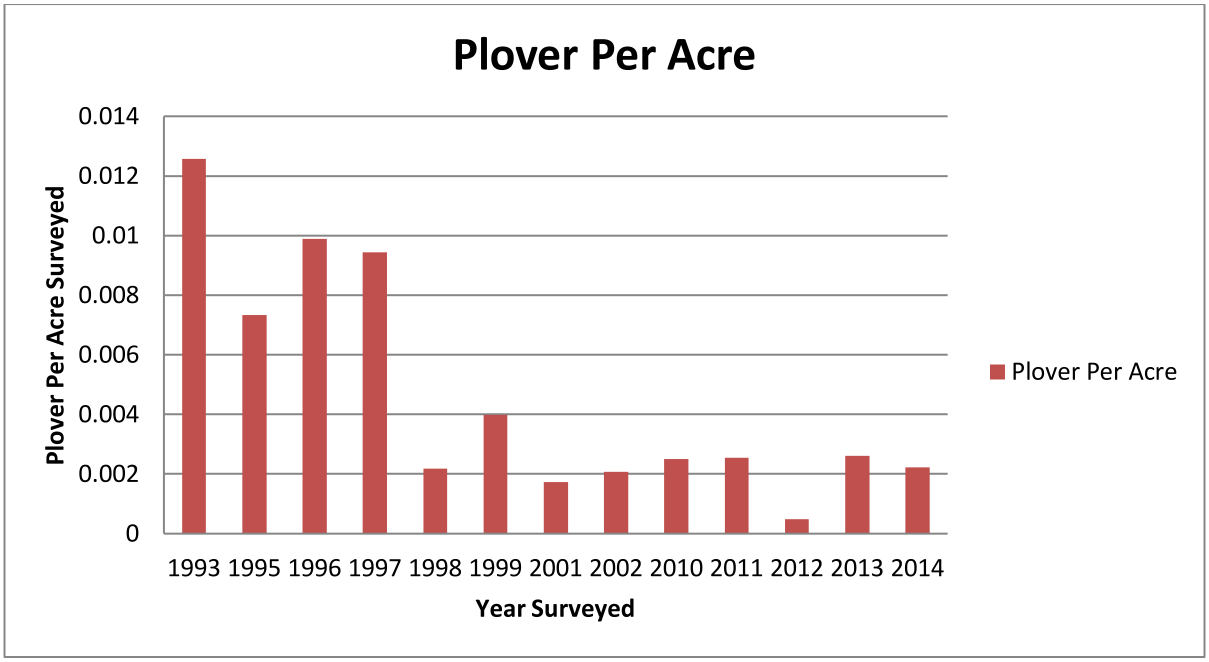
- 2011 – 17 sites
- 2012 – 17 sites
- 2013 – 17 sites

2014 – Sites were identified and the first year of data was collected. This monitoring is being analyzed and completed by the Douglas Range Staff.

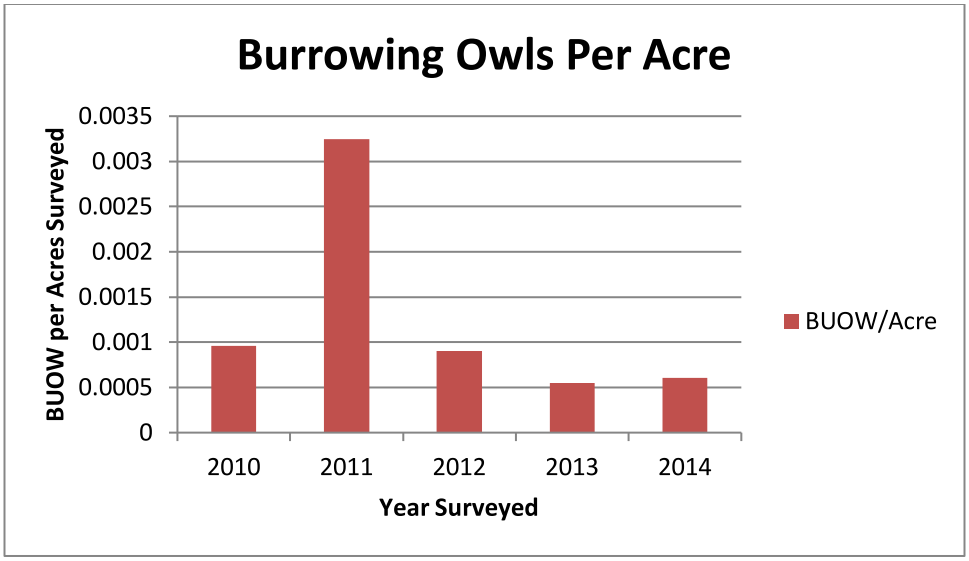
ASSOCIATED SPECIES SURVYES

The black-tailed prairie dog (BTPD) has garnered much attention as a species of conservation concern given that it only occupies 2% of its historical range in North America and only 0.01% of its former range in Wyoming. Although the species itself is not in immediate danger of extinction, the unique ecosystem they create is jeopardized by continuing fragmentation, isolation, and species persecution. Prairie dogs are considered a keystone species because the habitat they create cannot be duplicated by another species and is required, either directly or indirectly, by other wildlife. For these reasons, there continues to be widespread concern for the viability of species associated with BTPDs in Wyoming and on Thunder Basin National Grassland (TBNG). Associated species of immediate conservation concern include the Mountain Plover (*Charadrius montanus*), Burrowing Owl (*Athene cunicularia*), swift fox (*Vulpes velox*), and and the black-footed ferret (*Mustela nigripes*).

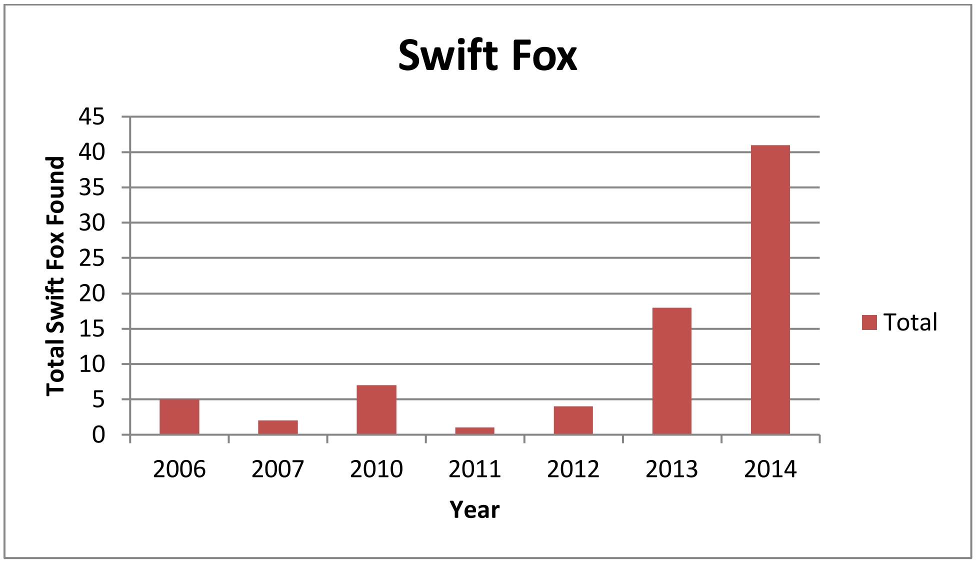
MOUNTAIN PLOVER



BURROWING OWL

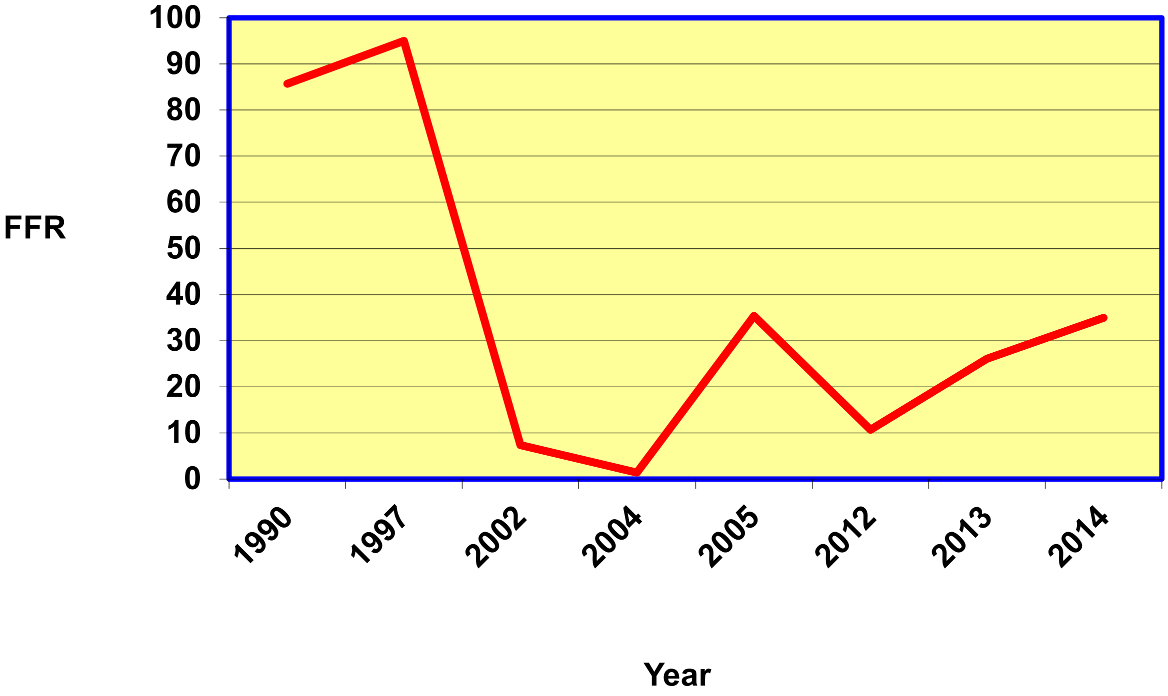


SWIFT FOX



FERRET FAMILY RATING FOR THUNDER BASIN NG

Ferret family ratings are used to determine approximately how many ferrets a prairie dog complex can support over times. Occupied acres and burrow density data are used in the formula to determine a FFR. A ferret family is defined by Biggins (1993) as the number of ferret families a prairie dog complex can support for one year (1 female, 3.3 young and 0.5 male).



2014 COST ESTIMATES

Mapping - $12,000
Dusting - $42,000
Associated Species Surveys - $14,000
Rodenticide - Cost: $ 20,140
Vegetation Monitoring - $2,000

Total Prairie Dog Management Expenses --- $ 90,140

FS Funds Expended	$ 59,140
Non-FS Funds Expended	$ 31,000

	% Of Total Cost	% Of FS Cost
➢ Mapping	13%	20%
➢ Associated Species Survyes	16%	24%
➢ Dusting – FS expenses	12%	19%
➢ Dusting – NGO expenses	34%	
➢ Rodenticide	22%	34%
➢ Vegetation Monitoring	2%	3%

NATIONAL BALD EAGLE MANAGEMENT GUIDELINES

U.S. Fish and Wildlife Service

May 2007

TABLE OF CONTENTS

INTRODUCTION

The bald eagle (*Haliaeetus leucocephalus*) is protected by the Bald and Golden Eagle Protection Act (Eagle Act) and the Migratory Bird Treaty Act (MBTA). The MBTA and the Eagle Act protect bald eagles from a variety of harmful actions and impacts. The U.S. Fish and Wildlife Service (Service) developed these National Bald Eagle Management Guidelines to advise landowners, land managers, and others who share public and private lands with bald eagles when and under what circumstances the protective provisions of the Eagle Act may apply to their activities. A variety of human activities can potentially interfere with bald eagles, affecting their ability to forage, nest, roost, breed, or raise young. The Guidelines are intended to help people minimize such impacts to bald eagles, particularly where they may constitute “disturbance,” which is prohibited by the Eagle Act.

The Guidelines are intended to:

(1) Publicize the provisions of the Eagle Act that continue to protect bald eagles, in order to reduce the possibility that people will violate the law,

(2) Advise landowners, land managers and the general public of the potential for various human activities to disturb bald eagles, and

(3) Encourage additional nonbinding land management practices that benefit bald eagles (see Additional Recommendations section).

While the Guidelines include general recommendations for land management practices that will benefit bald eagles, the document is intended primarily as a tool for landowners and planners who seek information and recommendations regarding how to avoid disturbing bald eagles. Many States and some tribal entities have developed state-specific management plans, regulations, and/or guidance for landowners and land managers to protect and enhance bald eagle habitat, and we encourage the continued development and use of these planning tools to benefit bald eagles.

Adherence to the Guidelines herein will benefit individuals, agencies, organizations, and companies by helping them avoid violations of the law. However, the Guidelines themselves are not law. Rather, they are recommendations based on several decades of behavioral observations, science, and conservation measures to avoid or minimize adverse impacts to bald eagles.

The U.S. Fish and Wildlife Service strongly encourages adherence to these guidelines to ensure that bald and golden eagle populations will continue to be sustained. The Service realizes there may be impacts to some birds even if all reasonable measures are taken to avoid such impacts. Although it is not possible to absolve individuals and entities from liability under the Eagle Act or the MBTA, the Service exercises enforcement discretion to focus on those individuals, companies, or agencies that take migratory birds without regard for the consequences of their actions and the law, especially when conservation measures, such as these Guidelines, are available, but have not been implemented. The Service will prioritize its enforcement efforts to focus on those individuals or entities who take bald eagles or their parts, eggs, or nests without implementing appropriate measures recommended by the Guidelines.

The Service intends to pursue the development of regulations that would authorize, under limited circumstances, the use of permits if "take" of an eagle is anticipated but unavoidable. Additionally, if the bald eagle is delisted, the Service intends to provide a regulatory mechanism to honor existing (take) authorizations under the Endangered Species Act (ESA).

During the interim period until the Service completes a rulemaking for permits under the Eagle Act, the Service does not intend to refer for prosecution the incidental "*take*" of any bald eagle under the MBTA or Eagle Act, if such take is in full compliance with the terms and conditions of an incidental take statement issued to the action agency or applicant under the authority of section 7(b)(4) of the ESA or a permit issued under the authority of section 10(a)(1)(B) of the ESA.

The Guidelines are applicable throughout the United States, including Alaska. The primary purpose of these Guidelines is to provide information that will minimize or prevent violations only of *Federal* laws governing bald eagles. In addition to Federal laws, many states and some smaller jurisdictions and tribes have additional laws and regulations protecting bald eagles. In some cases those laws and regulations may be more protective (restrictive) than these Federal guidelines. If you are planning activities that may affect bald eagles, we therefore recommend that you contact both your nearest U.S. Fish and Wildlife Service Field Office (see the contact information on p.16) and your state wildlife agency for assistance.

LEGAL PROTECTIONS FOR THE BALD EAGLE

The Bald and Golden Eagle Protection Act

The Eagle Act (16 U.S.C. 668-668c), enacted in 1940, and amended several times since then, prohibits anyone, without a permit issued by the Secretary of the Interior, from "taking" bald eagles, including their parts, nests, or eggs. The Act provides criminal and civil penalties for persons who "take, possess, sell, purchase, barter, offer to sell, purchase or barter, transport, export or import, at any time or any manner, any bald eagle ... [or any golden eagle], alive or dead, or any part, nest, or egg thereof." The Act defines "take" as "pursue, shoot, shoot at, poison, wound, kill, capture, trap, collect, molest or disturb." "Disturb'' means:

> "Disturb means to agitate or bother a bald or golden eagle to a degree that causes, or is likely to cause, based on the best scientific information available, 1) injury to an eagle, 2) a decrease in its productivity, by substantially interfering with normal breeding, feeding, or sheltering behavior, or 3) nest abandonment, by substantially interfering with normal breeding, feeding, or sheltering behavior."

In addition to immediate impacts, this definition also covers impacts that result from human-induced alterations initiated around a previously used nest site during a time when eagles are not present, if, upon the eagle=s return, such alterations agitate or bother an eagle to a degree that injures an eagle or substantially interferes with normal breeding, feeding, or sheltering habits and causes, or is likely to cause, a loss of productivity or nest abandonment.

A violation of the Act can result in a criminal fine of $100,000 ($200,000 for organizations), imprisonment for one year, or both, for a first offense. Penalties increase substantially for additional offenses, and a second violation of this Act is a felony.

The Migratory Bird Treaty Act
The MBTA (16 U.S.C. 703-712), prohibits the taking of any migratory bird or any part, nest, or egg, except as permitted by regulation. The MBTA was enacted in 1918; a 1972 agreement supplementing one of the bilateral treaties underlying the MBTA had the effect of expanding the scope of the Act to cover bald eagles and other raptors. Implementing regulations define “take” under the MBTA as “pursue, hunt, shoot, wound, kill, trap, capture, possess, or collect.”

Copies of the Eagle Act and the MBTA are available at: http://permits.fws.gov/ltr/ltr.shtml.

State laws and regulations
Most states have their own regulations and/or guidelines for bald eagle management. Some states may continue to list the bald eagle as endangered, threatened, or of special concern. If you plan activities that may affect bald eagles, we urge you to familiarize yourself with the regulations and/or guidelines that apply to bald eagles in your state. Your adherence to the Guidelines herein does not ensure that you are in compliance with state laws and regulations because state regulations can be more specific and/or restrictive than these Guidelines.

NATURAL HISTORY OF THE BALD EAGLE

Bald eagles are a North American species that historically occurred throughout the contiguous United States and Alaska. After severely declining in the lower 48 States between the 1870s and the 1970s, bald eagles have rebounded and re-established breeding territories in each of the lower 48 states. The largest North American breeding populations are in Alaska and Canada, but there are also significant bald eagle populations in Florida, the Pacific Northwest, the Greater Yellowstone area, the Great Lakes states, and the Chesapeake Bay region. Bald eagle distribution varies seasonally. Bald eagles that nest in southern latitudes frequently move northward in late spring and early summer, often summering as far north as Canada. Most eagles that breed at northern latitudes migrate southward during winter, or to coastal areas where waters remain unfrozen. Migrants frequently concentrate in large numbers at sites where food is abundant and they often roost together communally. In some cases, concentration areas are used year-round: in summer by southern eagles and in winter by northern eagles.

Juvenile bald eagles have mottled brown and white plumage, gradually acquiring their dark brown body and distinctive white head and tail as they mature. Bald eagles generally attain adult plumage by 5 years of age. Most are capable of breeding at 4 or 5 years of age, but in healthy populations they may not start breeding until much older. Bald eagles may live 15 to 25 years in the wild. Adults weigh 8 to 14 pounds (occasionally reaching 16 pounds in Alaska) and have wingspans of 5 to 8 feet. Those in the northern range are larger than those in the south, and females are larger than males.

Where do bald eagles nest?

Breeding bald eagles occupy "territories," areas they will typically defend against intrusion by other eagles. In addition to the active nest, a territory may include one or more alternate nests (nests built or maintained by the eagles but not used for nesting in a given year). The Eagle Act prohibits removal or destruction of both active and alternate bald eagle nests. Bald eagles exhibit high nest site fidelity and nesting territories are often used year after year. Some territories are known to have been used continually for over half a century.

Bald eagles generally nest near coastlines, rivers, large lakes or streams that support an adequate food supply. They often nest in mature or old-growth trees; snags (dead trees); cliffs; rock promontories; rarely on the ground; and with increasing frequency on human-made structures such as power poles and communication towers. In forested areas, bald eagles often select the tallest trees with limbs strong enough to support a nest that can weigh more than 1,000 pounds. Nest sites typically include at least one perch with a clear view of the water where the eagles usually forage. Shoreline trees or snags located in reservoirs provide the visibility and accessibility needed to locate aquatic prey. Eagle nests are constructed with large sticks, and may be lined with moss, grass, plant stalks, lichens, seaweed, or sod. Nests are usually about 4-6 feet in diameter and 3 feet deep, although larger nests exist.

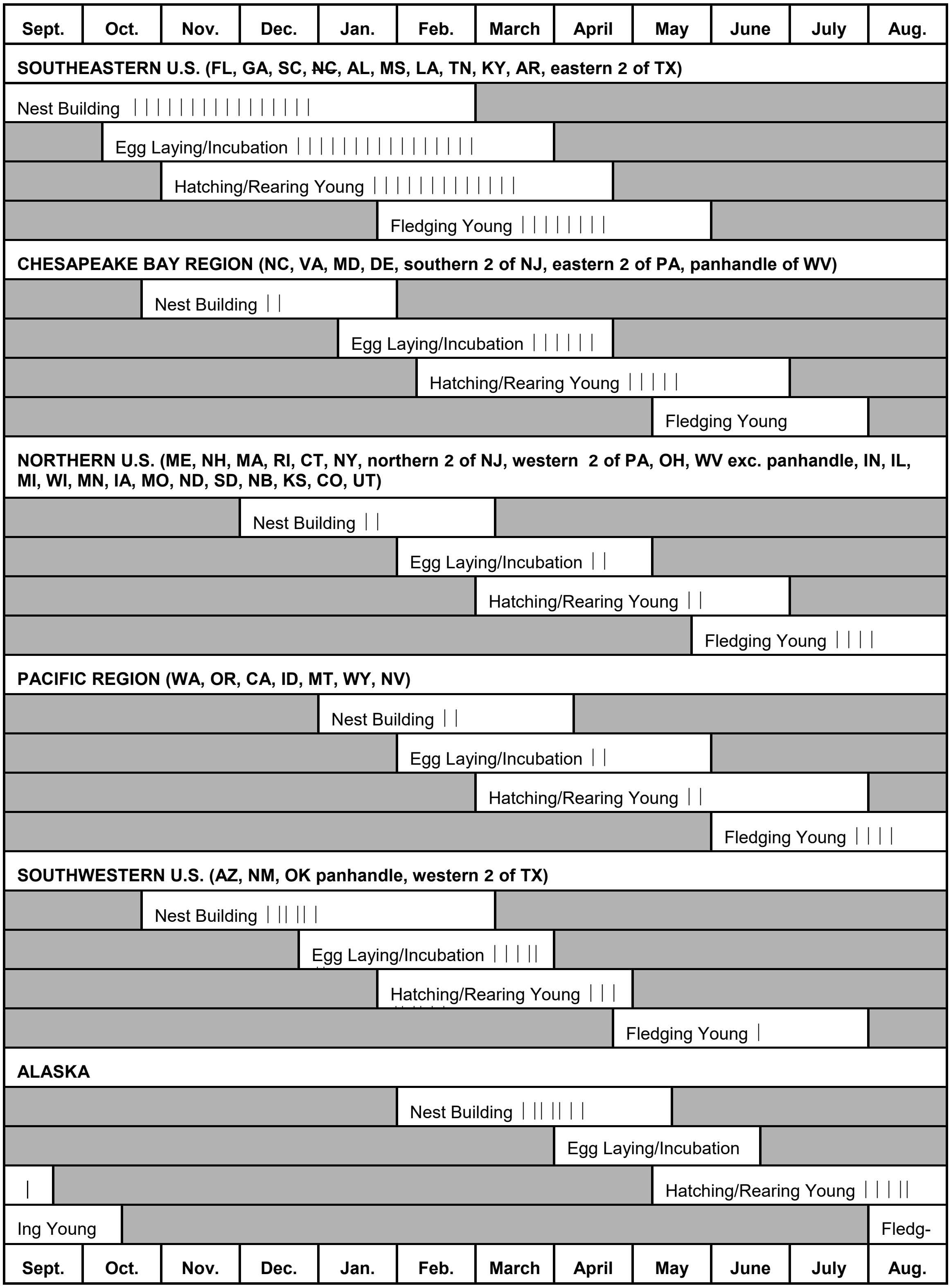
The range of breeding bald eagles in 2000 (shaded areas). This map shows only the larger concentrations of nests; eagles have continued to expand into additional nesting territories in many states. The dotted line represents the bald eagle's wintering range.

When do bald eagles nest?

Nesting activity begins several months before egg-laying. Egg-laying dates vary throughout the U.S., ranging from October in Florida, to late April or even early May in the northern United States. Incubation typically lasts 33-35 days, but can be as long as 40 days. Eaglets make their first unsteady flights about 10 to 12 weeks after hatching, and fledge (leave their nests) within a few days after that first flight. However, young birds usually remain in the vicinity of the nest for several weeks after fledging because they are almost completely dependent on their parents for food until they disperse from the nesting territory approximately 6 weeks later.

The bald eagle breeding season tends to be longer in the southern U.S., and re-nesting following an unsuccessful first nesting attempt is more common there as well. The following table shows the timing of bald eagle breeding seasons in different regions of the country. The table represents the range of time within which the majority of nesting activities occur in each region and does not apply to any specific nesting pair. Because the timing of nesting activities may vary within a given region, you should contact the nearest U.S. Fish and Wildlife Service Field Office (see page 16) and/or your state wildlife conservation agency for more specific information on nesting chronology in your area.

Chronology of typical reproductive activities of bald eagles in the United States.



How many chicks do bald eagles raise?

The number of eagle eggs laid will vary from 1-3, with 1-2 eggs being the most common. Only one eagle egg is laid per day, although not always on successive days. Hatching of young occurs on different days with the result that chicks in the same nest are sometimes of unequal size. The overall national fledging rate is approximately one chick per nest, annually, which results in a healthy expanding population.

What do bald eagles eat?

Bald eagles are opportunistic feeders. Fish comprise much of their diet, but they also eat waterfowl, shorebirds/colonial waterbirds, small mammals, turtles, and carrion. Because they are visual hunters, eagles typically locate their prey from a conspicuous perch, or soaring flight, then swoop down and strike. Wintering bald eagles often congregate in large numbers along streams to feed on spawning salmon or other fish species, and often gather in large numbers in areas below reservoirs, especially hydropower dams, where fish are abundant. Wintering eagles also take birds from rafts of ducks at reservoirs and rivers, and congregate on melting ice shelves to scavenge dead fish from the current or the soft melting ice. Bald eagles will also feed on carcasses along roads, in landfills, and at feedlots.

During the breeding season, adults carry prey to the nest to feed the young. Adults feed their chicks by tearing off pieces of food and holding them to the beaks of the eaglets. After fledging, immature eagles are slow to develop hunting skills, and must learn to locate reliable food sources and master feeding techniques. Young eagles will congregate together, often feeding upon easily acquired food such as carrion and fish found in abundance at the mouths of streams and shallow bays and at landfills.

The impact of human activity on nesting bald eagles

During the breeding season, bald eagles are sensitive to a variety of human activities. However, not all bald eagle pairs react to human activities in the same way. Some pairs nest successfully just dozens of yards from human activity, while others abandon nest sites in response to activities much farther away. This variability may be related to a number of factors, including visibility, duration, noise levels, extent of the area affected by the activity, prior experiences with humans, and tolerance of the individual nesting pair. The relative sensitivity of bald eagles during various stages of the breeding season is outlined in the following table.

Nesting Bald Eagle Sensitivity to Human Activities

Phase	Activity	Sensitivity to Human Activity	Comments
I	Courtship and Nest Building	Most sensitive period; likely to respond negatively	Most critical time period. Disturbance is manifested in nest abandonment. Bald eagles in newly established territories are more prone to abandon nest sites.
II	Egg laying	Very sensitive period	Human activity of even limited duration may cause nest desertion and abandonment of territory for the breeding season.
III	Incubation and early nestling period (up to 4 weeks)	Very sensitive period	Adults are less likely to abandon the nest near and after hatching. However, flushed adults leave eggs and young unattended; eggs are susceptible to cooling, loss of moisture, overheating, and predation; young are vulnerable to elements.
IV	Nestling period, 4 to 8 weeks	Moderately sensitive period	Likelihood of nest abandonment and vulnerability of the nestlings to elements somewhat decreases. However, nestlings may miss feedings, affecting their survival.
V	Nestlings 8 weeks through fledging	Very sensitive period	Gaining flight capability, nestlings 8 weeks and older may flush from the nest prematurely due to disruption and die.

If agitated by human activities, eagles may inadequately construct or repair their nest, may expend energy defending the nest rather than tending to their young, or may abandon the nest altogether. Activities that cause prolonged absences of adults from their nests can jeopardize eggs or young. Depending on weather conditions, eggs may overheat or cool too much and fail to hatch. Unattended eggs and nestlings are subject to predation. Young nestlings are particularly vulnerable because they rely on their parents to provide warmth or shade, without which they may die as a result of hypothermia or heat stress. If food delivery schedules are interrupted, the young may not develop healthy plumage, which can affect their survival. In addition, adults startled while incubating or brooding young may damage eggs or injure their young as they abruptly leave the nest. Older nestlings no longer require constant attention from the adults, but they may be startled by loud or intrusive human activities and prematurely jump from the nest before they are able to fly or care for themselves. Once fledged, juveniles range up to ¼ mile from the nest site, often to a site with minimal human activity. During this period, until about six weeks after departure from the nest, the juveniles still depend on the adults to feed them.

The impact of human activity on foraging and roosting bald eagles

Disruption, destruction, or obstruction of roosting and foraging areas can also negatively affect bald eagles. Disruptive activities in or near eagle foraging areas can interfere with feeding, reducing chances of survival. Interference with feeding can also result in reduced productivity (number of young successfully fledged). Migrating and wintering bald eagles often congregate at specific sites for purposes of feeding and sheltering. Bald eagles rely on established roost sites because of their proximity to sufficient food sources. Roost sites are usually in mature trees where the eagles are somewhat sheltered from the wind and weather. Human activities near or within communal roost sites may prevent eagles from feeding or taking shelter, especially if there are not other undisturbed and productive feeding and roosting sites available. Activities that permanently alter communal roost sites and important foraging areas can altogether eliminate the elements that are essential for feeding and sheltering eagles.

Where a human activity agitates or bothers roosting or foraging bald eagles to the degree that causes injury or substantially interferes with breeding, feeding, or sheltering behavior and causes, or is likely to cause, a loss of productivity or nest abandonment, the conduct of the activity constitutes a violation of the Eagle Act's prohibition against disturbing eagles. The circumstances that might result in such an outcome are difficult to predict without detailed site-specific information. If your activities may disturb roosting or foraging bald eagles, you should contact your local Fish and Wildlife Service Field Office (see page 16) for advice and recommendations for how to avoid such disturbance.

RECOMMENDATIONS FOR AVOIDING DISTURBANCE AT NEST SITES

In developing these Guidelines, we relied on existing state and regional bald eagle guidelines, scientific literature on bald eagle disturbance, and recommendations of state and Federal biologists who monitor the impacts of human activity on eagles. Despite these resources, uncertainties remain regarding the effects of many activities on eagles and how eagles in different situations may or may not respond to certain human activities. The Service recognizes this uncertainty and views the collection of better biological data on the response of eagles to disturbance as a high priority. To the extent that resources allow, the Service will continue to collect data on responses of bald eagles to human activities conducted according to the recommendations within these Guidelines to ensure that adequate protection from disturbance is being afforded, and to identify circumstances where the Guidelines might be modified. These data will be used to make future adjustments to the Guidelines.

To avoid disturbing nesting bald eagles, we recommend (1) keeping a distance between the activity and the nest (distance buffers), (2) maintaining preferably forested (or natural) areas between the activity and around nest trees (landscape buffers), and (3) avoiding certain activities during the breeding season. The buffer areas serve to minimize visual and auditory impacts associated with human activities near nest sites. Ideally, buffers would be large enough to protect existing nest trees and provide for alternative or replacement nest trees.

The size and shape of effective buffers vary depending on the topography and other ecological characteristics surrounding the nest site. In open areas where there are little or no forested or topographical buffers, such as in many western states, distance alone must serve as the buffer. Consequently, in open areas, the distance between the activity and the nest may need to be larger than the distances recommended under Categories A and B of these guidelines (pg. 12) if no landscape buffers are present. The height of the nest above the ground may also ameliorate effects of human activities; eagles at higher nests may be less prone to disturbance.

In addition to the physical features of the landscape and nest site, the appropriate size for the distance buffer may vary according to the historical tolerances of eagles to human activities in particular localities, and may also depend on the location of the nest in relation to feeding and roosting areas used by the eagles. Increased competition for nest sites may lead bald eagles to nest closer to human activity (and other eagles).

Seasonal restrictions can prevent the potential impacts of many shorter-term, obtrusive activities that do not entail landscape alterations (e.g. fireworks, outdoor concerts). In proximity to the nest, these kinds of activities should be conducted only outside the breeding season. For activities that entail both short-term, obtrusive characteristics and more permanent impacts (e.g., building construction), we recommend a combination of both approaches: retaining a landscape buffer *and* observing seasonal restrictions.

For assistance in determining the appropriate size and configuration of buffers or the timing of activities in the vicinity of a bald eagle nest, we encourage you to contact the nearest U.S. Fish and Wildlife Service Field Office (see page 16).

Existing Uses

Eagles are unlikely to be disturbed by routine use of roads, homes, and other facilities where such use pre-dates the eagles' successful nesting activity in a given area. Therefore, in most cases *ongoing* existing uses may proceed with the same intensity with little risk of disturbing bald eagles. However, some *intermittent, occasional, or irregular* uses that pre-date eagle nesting in an area may disturb bald eagles. For example: a pair of eagles may begin nesting in an area and subsequently be disturbed by activities associated with an annual outdoor flea market, even though the flea market has been held annually at the same location. In such situations, human activity should be adjusted or relocated to minimize potential impacts on the nesting pair.

ACTIVITY-SPECIFIC GUIDELINES

The following section provides the Service=s management recommendations for avoiding bald eagle disturbance as a result of new or intermittent activities proposed in the vicinity of bald eagle nests. Activities are separated into 8 categories (A – H) based on the nature and magnitude of impacts to bald eagles that usually result from the type of activity. Activities with similar or comparable impacts are grouped together.

In most cases, impacts will vary based on the visibility of the activity from the eagle nest and the degree to which similar activities are already occurring in proximity to the nest site. Visibility is a factor because, in general, eagles are more prone to disturbance when an activity occurs in full view. For this reason, we recommend that people locate activities farther from the nest structure in areas with open vistas, in contrast to areas where the view is shielded by rolling topography, trees, or other screening factors. The recommendations also take into account the existence of similar activities in the area because the continued presence of nesting bald eagles in the vicinity of the existing activities indicates that the eagles in that area can tolerate a greater degree of human activity than we can generally expect from eagles in areas that experience fewer human impacts. To illustrate how these factors affect the likelihood of disturbing eagles, we have incorporated the recommendations for some activities into a table (categories A and B).

First, determine which category your activity falls into (between categories A – H). If the activity you plan to undertake is not specifically addressed in these guidelines, follow the recommendations for the most similar activity represented.

If your activity is under A or B, our recommendations are in table form. The vertical axis shows the degree of visibility of the activity from the nest. The horizontal axis (header row) represents the degree to which similar activities are ongoing in the vicinity of the nest. Locate the row that best describes how visible your activity will be from the eagle nest. Then, choose the column that best describes the degree to which similar activities are ongoing in the vicinity of the eagle nest. The box where the column and row come together contains our management recommendations for how far you should locate your activity from the nest to avoid disturbing the eagles. The numerical distances shown in the tables are the closest the activity should be conducted relative to the nest. In some cases we have included additional recommendations (other than recommended *distance* from the nest) you should follow to help ensure that your activity will not disturb the eagles.

Alternate nests
For activities that entail permanent landscape alterations that may result in bald eagle disturbance, these recommendations apply to both active and alternate bald eagle nests. Disturbance becomes an issue with regard to alternate nests if eagles return for breeding purposes and react to land use changes that occurred while the nest was inactive. The likelihood that an alternate nest will again become active decreases the longer it goes unused. If you plan activities in the vicinity of an alternate bald eagle nest and have information to show that the nest has not been active during the preceding 5 breeding seasons, the recommendations provided in these guidelines for avoiding disturbance around the nest site may no longer be warranted. The nest itself remains protected by other provisions of the Eagle Act, however, and may not be destroyed.

If special circumstances exist that make it unlikely an inactive nest will be reused before 5 years of disuse have passed, and you believe that the probability of reuse is low enough to warrant disregarding the recommendations for avoiding disturbance, you should be prepared to provide all the reasons for your conclusion, including information regarding past use of the nest site. Without sufficient documentation, you should continue to follow these guidelines when conducting activities around the nest site. If we are able to determine that it is unlikely the nest will be reused, we may advise you that the recommendations provided in these guidelines for avoiding disturbance are no longer necessary around that nest site.

This guidance is intended to minimize disturbance, as defined by Federal regulation. In addition to Federal laws, most states and some tribes and smaller jurisdictions have additional laws and regulations protecting bald eagles. In some cases those laws and regulations may be more protective (restrictive) than these Federal guidelines.

Temporary Impacts
For activities that have temporary impacts, such as the use of loud machinery, fireworks displays, or summer boating activities, we recommend seasonal restrictions. These types of activities can generally be carried out outside of the breeding season without causing disturbance. The recommended restrictions for these types of activities can be lifted for alternate nests within a particular territory, including nests that were attended during the current breeding season but not used to raise young, after eggs laid in another nest within the territory have hatched (depending on the distance between the alternate nest and the active nest).

In general, activities should be kept as far away from nest trees as possible; loud and disruptive activities should be conducted when eagles are not nesting; and activity between the nest and the nearest foraging area should be minimized. If the activity you plan to undertake is not specifically addressed in these guidelines, follow the recommendations for the most similar activity addressed, or contact your local U.S. Fish and Wildlife Service Field Office for additional guidance.

If you believe that special circumstances apply to your situation that increase or diminish the likelihood of bald eagle disturbance, or if it is not possible to adhere to the guidelines, you should contact your local Service Field Office for further guidance.

Category A:
Building construction, 1 or 2 story, with project footprint of ½ acre or less.
Construction of roads, trails, canals, power lines, and other linear utilities.
Agriculture and aquaculture – new or expanded operations.
Alteration of shorelines or wetlands.
Installation of docks or moorings.
Water impoundment.

Category B:
Building construction, 3 or more stories.
Building construction, 1 or 2 story, with project footprint of more than ½ acre.
Installation or expansion of marinas with a capacity of 6 or more boats.
Mining and associated activities.
Oil and natural gas drilling and refining and associated activities.

	If there is no similar activity within 1 mile of the nest	***If there is similar activity closer than 1 mile from the nest***
If the activity will be visible from the nest	660 feet. Landscape buffers are recommended.	660 feet, or as close as existing tolerated activity of similar scope. Landscape buffers are recommended.
If the activity will not be visible from the nest	Category A: 330 feet. Clearing, external construction, and landscaping between 330 feet and 660 feet should be done outside breeding season. Category B: 660 feet.	330 feet, or as close as existing tolerated activity of similar scope. Clearing, external construction and landscaping within 660 feet should be done outside breeding season.

The numerical distances shown in the table are the closest the activity should be conducted relative to the nest.

Category C. Timber Operations and Forestry Practices

- Avoid clear cutting or removal of overstory trees within 330 feet of the nest at any time.

- Avoid timber harvesting operations, including road construction and chain saw and yarding operations, during the breeding season within 660 feet of the nest. The distance may be decreased to 330 feet around alternate nests within a particular territory, including nests that were attended during the current breeding season but not used to raise young, after eggs laid in another nest within the territory have hatched.

- Selective thinning and other silviculture management practices designed to conserve or enhance habitat, including prescribed burning close to the nest tree, should be undertaken outside the breeding season. Precautions such as raking leaves and woody debris from around the nest tree should be taken to prevent crown fire or fire climbing the nest tree. If it is determined that a burn during the breeding season would be beneficial, then, to ensure that no take or disturbance will occur, these activities should be conducted only when neither adult eagles nor young are present at the nest tree (i.e., at the beginning of, or end of, the breeding season, either before the particular nest is active or after the young have fledged from that nest). Appropriate Federal and state biologists should be consulted before any prescribed burning is conducted during the breeding season.

- Avoid construction of log transfer facilities and in-water log storage areas within 330 feet of the nest.

Category D. Off-road vehicle use (including snowmobiles). No buffer is necessary around nest sites outside the breeding season. During the breeding season, do not operate off-road vehicles within 330 feet of the nest. In open areas, where there is increased visibility and exposure to noise, this distance should be extended to 660 feet.

Category E. Motorized Watercraft use (including jet skis/personal watercraft). No buffer is necessary around nest sites outside the breeding season. During the breeding season, within 330 feet of the nest, (1) do not operate jet skis (personal watercraft), and (2) avoid concentrations of noisy vessels (e.g., commercial fishing boats and tour boats), except where eagles have demonstrated tolerance for such activity. Other motorized boat traffic passing within 330 feet of the nest should attempt to minimize trips and avoid stopping in the area where feasible, particularly where eagles are unaccustomed to boat traffic. Buffers for airboats should be larger than 330 feet due to the increased noise they generate, combined with their speed, maneuverability, and visibility.

Category F. Non-motorized recreation and human entry (e.g., hiking, camping, fishing, hunting, birdwatching, kayaking, canoeing). No buffer is necessary around nest sites outside the breeding season. If the activity will be visible or highly audible from the nest, maintain a 330-foot buffer during the breeding season, particularly where eagles are unaccustomed to such activity.

Category G. Helicopters and fixed-wing aircraft.
Except for authorized biologists trained in survey techniques, avoid operating aircraft within 1,000 feet of the nest during the breeding season, except where eagles have demonstrated tolerance for such activity.

Category H. Blasting and other loud, intermittent noises.
Avoid blasting and other activities that produce extremely loud noises within 1/2 mile of active nests, unless greater tolerance to the activity (or similar activity) has been demonstrated by the eagles in the nesting area. This recommendation applies to the use of fireworks classified by the Federal Department of Transportation as Class B explosives, which includes the larger fireworks that are intended for licensed public display.

RECOMMENDATIONS FOR AVOIDING DISTURBANCE AT FORAGING AREAS AND COMMUNAL ROOST SITES

1. Minimize potentially disruptive activities and development in the eagles' direct flight path between their nest and roost sites and important foraging areas.

2. Locate long-term and permanent water-dependent facilities, such as boat ramps and marinas, away from important eagle foraging areas.

3. Avoid recreational and commercial boating and fishing near critical eagle foraging areas during peak feeding times (usually early to mid-morning and late afternoon), except where eagles have demonstrated tolerance to such activity.

4. Do not use explosives within ½ mile (or within 1 mile in open areas) of communal roosts when eagles are congregating, without prior coordination with the U.S. Fish and Wildlife Service and your state wildlife agency.

5. Locate aircraft corridors no closer than 1,000 feet vertical or horizontal distance from communal roost sites.

ADDITIONAL RECOMMENDATIONS TO BENEFIT BALD EAGLES

The following are additional management practices that landowners and planners can exercise for added benefit to bald eagles.

1. Protect and preserve potential roost and nest sites by retaining mature trees and old growth stands, particularly within ½ mile from water.

2. Where nests are blown from trees during storms or are otherwise destroyed by the elements, continue to protect the site in the absence of the nest for up to three (3) complete breeding seasons. Many eagles will rebuild the nest and reoccupy the site.

3. To avoid collisions, site wind turbines, communication towers, and high voltage transmission power lines away from nests, foraging areas, and communal roost sites.

4. Employ industry-accepted best management practices to prevent birds from colliding with or being electrocuted by utility lines, towers, and poles. If possible, bury utility lines in important eagle areas.

5. Where bald eagles are likely to nest in human-made structures (e.g., cell phone towers) and such use could impede operation or maintenance of the structures or jeopardize the safety of the eagles, equip the structures with either (1) devices engineered to discourage bald eagles from building nests, or (2) nesting platforms that will safely accommodate bald eagle nests without interfering with structure performance.

6. Immediately cover carcasses of euthanized animals at landfills to protect eagles from being poisoned.

7. Do not intentionally feed bald eagles. Artificially feeding bald eagles can disrupt their essential behavioral patterns and put them at increased risk from power lines, collision with windows and cars, and other mortality factors.

8. Use pesticides, herbicides, fertilizers, and other chemicals only in accordance with Federal and state laws.

9. Monitor and minimize dispersal of contaminants associated with hazardous waste sites (legal or illegal), permitted releases, and runoff from agricultural areas, especially within watersheds where eagles have shown poor reproduction or where bioaccumulating contaminants have been documented. These factors present a risk of contamination to eagles and their food sources.

CONTACTS

The following U.S. Fish and Wildlife Service Field Offices provide technical assistance on bald eagle management:

Alabama	Daphne	(251) 441-5181
Alaska	Anchorage	(907) 271-2888
	Fairbanks	(907) 456-0203
	Juneau	(907) 780-1160
Arizona	Phoenix	(602) 242-0210
Arkansas	Conway	(501) 513-4470
California	Arcata	(707) 822-7201
	Barstow	(760) 255-8852
	Carlsbad	(760) 431-9440
	Red Bluff	(530) 527-3043
	Sacramento	(916) 414-6000
	Stockton	(209) 946-6400
	Ventura	(805) 644-1766
	Yreka	(530) 842-5763
Colorado	Lakewood	(303) 275-2370
	Grand Junction	(970) 243-2778
Connecticut	(See New Hampshire)	
Delaware	(See Maryland)	
Florida	Panama City	(850) 769-0552
	Vero Beach	(772) 562-3909
	Jacksonville	(904) 232-2580
Georgia	Athens	(706) 613-9493
	Brunswick	(912) 265-9336
	Columbus	(706) 544-6428
Idaho	Boise	(208) 378-5243
	Chubbuck	(208) 237-6975
Illinois/Iowa	Rock Island	(309) 757-5800
Indiana	Bloomington	(812) 334-4261
Kansas	Manhattan	(785) 539-3474
Kentucky	Frankfort	(502) 695-0468
Louisiana	Lafayette	(337) 291-3100
Maine	Old Town	(207) 827-5938
Maryland	Annapolis	(410) 573-4573
Massachusetts	(See New Hampshire)	
Michigan	East Lansing	(517) 351-2555
Minnesota	Bloomington	(612) 725-3548
Mississippi	Jackson	(601) 965-4900
Missouri	Columbia	(573) 234-2132
Montana	Helena	(405) 449-5225
Nebraska	Grand Island	(308) 382-6468
Nevada	Las Vegas	(702) 515-5230
	Reno	(775) 861-6300

New Hampshire	Concord	(603) 223-2541
New Jersey	Pleasantville	(609) 646-9310
New Mexico	Albuquerque	(505) 346-2525
New York	Cortland	(607) 753-9334
	Long Island	(631) 776-1401
North Carolina	Raleigh	(919) 856-4520
	Asheville	(828) 258-3939
North Dakota	Bismarck	(701) 250-4481
Ohio	Reynoldsburg	(614) 469-6923
Oklahoma	Tulsa	(918) 581-7458
Oregon	Bend	(541) 383-7146
	Klamath Falls	(541) 885-8481
	La Grande	(541) 962-8584
	Newport	(541) 867-4558
	Portland	(503) 231-6179
	Roseburg	(541) 957-3474
Pennsylvania	State College	(814) 234-4090
Rhode Island	(See New Hampshire)	
South Carolina	Charleston	(843) 727-4707
South Dakota	Pierre	(605) 224-8693
Tennessee	Cookeville	(931) 528-6481
Texas	Clear Lake	(281) 286-8282
Utah	West Valley City	(801) 975-3330
Vermont	(See New Hampshire)	
Virginia	Gloucester	(804) 693-6694
Washington	Lacey	(306) 753-9440
	Spokane	(509) 891-6839
	Wenatchee	(509) 665-3508
West Virginia	Elkins	(304) 636-6586
Wisconsin	New Franken	(920) 866-1725
Wyoming	Cheyenne	(307) 772-2374
	Cody	(307) 578-5939

National Office
U.S. Fish and Wildlife Service
Division of Migratory Bird Management
4401 North Fairfax Drive, MBSP-4107
Arlington, VA 22203-1610
(703) 358-1714
http://www.fws.gov/migratorybirds

State Agencies

To contact a state wildlife agency, visit the Association of Fish & Wildlife Agencies' website at http://www.fishwildlife.org/where_us.html

GLOSSARY

The definitions below apply to these National Bald Eagle Management Guidelines:

Communal roost sites – Areas where bald eagles gather and perch overnight – and sometimes during the day in the event of inclement weather. Communal roost sites are usually in large trees (live or dead) that are relatively sheltered from wind and are generally in close proximity to foraging areas. These roosts may also serve a social purpose for pair bond formation and communication among eagles. Many roost sites are used year after year.

Disturb – To agitate or bother a bald or golden eagle to a degree that causes, or is likely to cause, based on the best scientific information available, 1) injury to an eagle, 2) a decrease in its productivity, by substantially interfering with normal breeding, feeding, or sheltering behavior, or 3) nest abandonment, by substantially interfering with normal breeding, feeding, or sheltering behavior.

In addition to immediate impacts, this definition also covers impacts that result from human-caused alterations initiated around a previously used nest site during a time when eagles are not present, if, upon the eagle=s return, such alterations agitate or bother an eagle to a degree that injures an eagle or substantially interferes with normal breeding, feeding, or sheltering habits and causes, or is likely to cause, a loss of productivity or nest abandonment.

Fledge – To leave the nest and begin flying. For bald eagles, this normally occurs at 10-12 weeks of age.

Fledgling – A juvenile bald eagle that has taken the first flight from the nest but is not yet independent.

Foraging area – An area where eagles feed, typically near open water such as rivers, lakes, reservoirs, and bays where fish and waterfowl are abundant, or in areas with little or no water (i.e., rangelands, barren land, tundra, suburban areas, etc.) where other prey species (e.g., rabbit, rodents) or carrion (such as at landfills) are abundant.

Landscape buffer – A natural or human-made landscape feature that screens eagles from human activity (e.g., strip of trees, hill, cliff, berm, sound wall).

Nest – A structure built, maintained, or used by bald eagles for the purpose of reproduction. An **active** nest is a nest that is attended (built, maintained or used) by a pair of bald eagles during a given breeding season, whether or not eggs are laid. An **alternate** nest is a nest that is not used for breeding by eagles during a given breeding season.

Nest abandonment – Nest abandonment occurs when adult eagles desert or stop attending a nest and do not subsequently return and successfully raise young in that nest for the duration of a breeding season. Nest abandonment can be caused by altering habitat near a nest, even if the alteration occurs prior to the breeding season. Whether the eagles migrate during the non-breeding season, or remain in the area throughout the non-breeding season, nest abandonment can occur at any point between the time the eagles return to the nesting site for the breeding season and the time when all progeny from the breeding season have dispersed.

Project footprint – The area of land (and water) that will be permanently altered for a development project, including access roads.

Similar scope – In the vicinity of a bald eagle nest, an existing activity is of similar scope to a new activity where the types of impacts to bald eagles are similar in nature, and the impacts of the existing activity are of the same or greater magnitude than the impacts of the potential new activity. Examples: (1) An existing single-story home 200 feet from a nest is similar in scope to an additional single-story home 200 feet from the nest; (2) An existing multi-story, multi-family dwelling 150 feet from a nest has impacts of a greater magnitude than a potential new single-family home 200 feet from the nest; (3) One existing single-family home 200 feet from the nest has impacts of a lesser magnitude than three single-family homes 200 feet from the nest; (4) an existing single-family home 200 feet from a communal roost has impacts of a lesser magnitude than a single-family home 300 feet from the roost but 40 feet from the eagles' foraging area. The existing activities in examples (1) and (2) are of similar scope, while the existing activities in example (3) and (4) are not.

Vegetative buffer – An area surrounding a bald eagle nest that is wholly or largely covered by forest, vegetation, or other natural ecological characteristics, and separates the nest from human activities.

RELATED LITERATURE

Andrew, J.M. and J.A. Mosher. 1981. Bald eagle nest site selection and nesting habitat in Maryland. Journal of Wildlife Management 46:382-390.

Anonymous. 1977. Bald Eagle Habitat Management Guidelines, Forest Service – California Region. U.S Forest Service, San Francisco, CA.

Anthony, R.G. 2001. Low productivity of bald eagles on Prince of Wales Island, southeast Alaska. Journal of Raptor Research 35:1-8.

Anthony, R.G., R.W. Frenzel, F.B. Isaacs, and M.G. Garrett. 1994. Probable causes of nesting failures in Oregon's bald eagle population. Wildlife Society Bulletin 22:576-582.

Anthony, R.G. and F.B. Isaacs. 1989. Characteristics of bald eagle nest sites in Oregon. Journal of Wildlife Management 53:148-158.

Arizona Game and Fish Department. 1999. Bald Eagle Conservation Assessment and Strategy (draft).

Avian Power Line Interaction Committee (APLIC). 1996. Suggested Practices for Raptor Protection on Power Lines: The State of the Art in 1996. Edison Electric Institute, Raptor Research Foundation, Washington, D.C.

Bangs, E.E., T.N. Bailey and V.D. Berns. Ecology of nesting bald eagles on the Kenai National Wildlife Refuge, Alaska. (USFWS staff)

Becker, J.M. 2002. Response of wintering bald eagles to industrial construction in southeastern Washington. Wildlife Society Bulletin 30:875-878.

Brauning, D.W. and J.D. Hassinger. 2000. Pennsylvania Recovery and Management Plan for the Bald Eagle (draft). Pennsylvania Game Commission. Harrisburg, PA.

Brown, B.T., G.S. Mills, C. Powels, W.A. Russell, G.D. Therres and J.J. Pottie. 1999. The influence of weapons-testing noise on bald eagle behavior. Journal of Raptor Research 33:227-232.

Brown, B.T. and L.E. Stevens. 1997. Winter bald eagle distribution is inversely correlated with human activity along the Colorado River, Arizona. Journal of Raptor Research31:7-10.

Buehler, D.A. 2000. Bald Eagle (*Haliaeetus leucocephalus*). *In* The Birds of North America, No. 506 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Buehler, D.A., T.J. Mersmann, J.D. Fraser, and J.K.D. Seegar. 1991. Effects of human activity on bald eagle distribution on the northern Chesapeake Bay. Journal of Wildlife Management 55:282-290.

Buehler, D.A., T.J. Mersmann, J.D. Fraser, and J.K.D. Seegar. 1991. Nonbreeding bald eagle communal and solitary roosting behavior and roost habitat on the northern Chesapeake Bay. Journal of Wildlife Management 55:273-281.

Chandler, SK., J.D. Fraser, D.A. Buehler and J.K.D. Seegar. 1995. Perch trees and shoreline development as predictors of bald eagle distribution on the Chesapeake Bay. Journal of Wildlife Management 59:325-332.

Cline, K. 1985. Bald Eagles in the Chesapeake: A Management Guide for Landowners. National Wildlife Federation. Washington, D.C.

Dell, D.D. and P.J. Zwank. 1986. Impact of a high-voltage transmission line on a nesting pair of southern bald eagles in southeast Louisiana. Journal of Raptor Research 20(3/4):117-119.

Dunwiddie, P.W. and R.C. Kuntz. 2001. Long-term trends of bald eagles in winter on the Skagit River, Washington. Journal of Wildlife Management 65(2):290-299.

Fletcher, R.J. et. al. 1999. Effects of recreational trails on wintering diurnal raptors along riparian corridors in a Colorado grassland. Journal of Raptor Research 33(3):233-239.

Fraser, J.D. 1981. The breeding biology and status of the bald eagle on the Chippewa National Forest. PhD. Dissertation, University of Minnesota.

Fraser, J.D., LD. Frenzel and J.E. Mathisen. 1985. The impact of human activities on breeding bald eagles in north-central Minnesota. Journal of Wildlife Management 49(3):585-592.

Garrett, M.G., J.W. Watson, and R.G. Anthony. 1993. Bald eagle home range and habitat use in the Columbia River Estuary. Journal of Wildlife Management 57(1):19-27.

Gerrard J.M. and G.R. Bortolotti. 1988. The Bald Eagle: Haunts and Habits of a Wilderness Monarch. Smithsonian Institution Press. Washington, D.C.

Grier, J.W. 1969. Bald eagle behavior and productivity responses to climbing to nests. Journal of Wildlife Management 33:961-966.

Grier, J.W. and J.E. Guinn. 2003. Bald eagle habitats and responses to human disturbance in Minnesota. Report to the Minnesota Department of Natural Resources.

Grubb, T.G. 1976. Survey and analysis of bald eagle nesting in western Washington. M.S. thesis, Univ. of Washington, Seattle.

Grubb, T.G. and R.M. King. 1991. Assessing human disturbance of breeding bald eagles with classification tree models. Journal of Wildlife Management 55:500-511.

Grubb, T.G., W.L. Robinson and W.W. Bowerman. 2002. Effects of watercraft on bald eagles nesting in Voyagers National Park, Minnesota. Wildlife Society Bulletin 30:156-161.

Grubb, T.G. and W.W. Bowerman. 1997. Variations in breeding bald eagle response to jets, light planes and helicopters. Journal of Raptor Research 31:213-222.

Grubb, T.G., W.W. Bowerman, A.J. Bath, J.P. Giesy, D.V.C. Weseloh. 2003. Evaluating Great Lakes bald eagle nesting habitat with Bayesian inference. RMRS-RP-45. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, 10 pp.

Hansen, J.A. 1977. Population dynamics and night roost requirements of bald eagles wintering in the Nooksack River Valley, WA. Huxley College of Environmental Studies, Western Washington State College, Bellingham, WA. (Problem Series)

Hansen, J.A., M.V. Stalmaster and J.R. Newman. 1980. Habitat characteristics, function, and destruction of bald eagle communal roosts in western Washington. Huxley college of Environmental Studies, Western Washington University.

Hunt, W.G., D.E. Driscoll, E.W. Bianchi, and R.E. Jackman. 1992. Ecology of bald eagles in Arizona. Report to U.S. Bureau of Reclamation, Contract 6-CS-30-04470. BioSystems Analysis Inc., Santa Cruz, California.

Isaacs, F.B and R.G. Anthony. 1987. Abundance, foraging, and roosting of bald eagles wintering in the Harney Basin, Oregon. Northwest Science 61(2), pp. 114-121.

Juenemann, B.G. 1973. Habitat evaluations of selected bald eagle nest sites on the Chippewa National Forest. M.S. thesis, University of Minnesota, Minneapolis.

Keister, G.P., R.G. Anthony and E.J. O'Neill. 1987. Use of communal roosts and foraging area by bald eagles wintering in the Klamath Basin. Journal of Wildlife Management 51(2):415-420.

Knight, R. and S.K. Knight. 1984. Responses of wintering bald eagles to boating activity. Journal of Wildlife Management 48:999-1004.

Linscombe, J.T., T.J. Hess, Jr., and V.L. Wright. 1999. Effects of seismic operations on Louisiana's nesting bald eagles. Proceedings of the Southeastern Association of Fish and Wildlife Agencies. 54:235-242.

Maine (State of) Inland Fisheries and Wildlife Rules. Chapter 8.05 Essential Habitat for Species Listed as Threatened or Endangered.

Mathisen, J.E. 1968. Effects of human disturbance on nesting bald eagles. Journal of Wildlife Management 32(1): 1-6.

McGarigal, K., R.G. Anthony and F.B. Isaacs. 1991. Interactions of humans and bald eagles on the Columbia River estuary. Wildlife Monographs 115:1-47.

McKay, K.J., J.W. Stravers, B.R. Conklin, U. Konig, S. Hawks, C.J. Kohrt, J.S. Lundh and G.V. Swenson. 2001. Potential human impacts on bald eagle reproductive success along the Upper Mississippi River.

McKewan, L.C. and D.H. Hirth. 1979. Southern bald eagle productivity and nest site selection. Journal of Wildlife Management 43:585-594.

Millsap, B.A. Status of wintering bald eagles in the conterminous 48 States. 1986. Wildlife Society Bulletin 14:433-440.

Millsap, B.A, T. Breen, E. McConnell, T. Steffer, L. Phillips, N. Douglass, and S. Taylor. In Press. Comparative fecundity and survival of bald eagles fledged from suburban and rural natal areas in Florida. Journal of Wildlife Management 68(4).

Montana Bald Eagle Working Group. 1986. Montana Bald Eagle Management Plan. Department of the Interior, Bureau of Land Management. Billings, MT.

Nesbitt, S.A., M.J. Folk and D.A. Wood. 1993. Effectiveness of bald eagle habitat protection guidelines in Florida. Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies.

Newman, J.R., W.H. Brennan and L.M. Smith. 1977. Twelve-year changes in nesting patterns of bald eagles on San Juan Island, Washington. The Murrelet 58(2)37-39.

Postapulsky, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. Pages 21-31 *in* F.N. Hammerstrom, Jr., B.E. Harrell, and R.R. Olendorff, eds. Management of raptors. Raptor Res. Found., Vermillion, S.D.

Rodgers, J.A. and Schwikert, S.T. 2003. Buffer zone distances to protect foraging and loafing waterbirds from disturbance by airboats in Florida. Waterbirds 26(4): 437-443.

Russell, D. 1980. Occurrence and human disturbance sensitivity of wintering bald eagles on the Sauk and Suiattle Rivers, Washington. In R.L. Knight, G.T. Allen, M.V. Stalmaster and C.W. Servheen [eds.]. Proceedings of the Washington Bald Eagle Symposium. Nature Conservancy, Seattle, Washington, pp. 165-174.

Shapiro, A.E., F. Montalbano, and D. Mager. 1982. Implications of construction of a flood control project upon bald eagle nesting activity. Wilson Bulletin 94(1), pp. 55-63.

Skagen, S.K. 1980. Behavioral responses of wintering bald eagles to human activity on the Skagit River, Washington. In R.L.Knight, G.T. Allen, M.V. Stalmaster and C.W. Servheen [eds.]. Proceedings of the Washington Bald Eagle Symposium. Nature Conservancy, Seattle, Washington, pp. 231-241.

Skagen, S.K., R.L. Knight and G.J.H. Orians. 1991. Human disturbance of an avian scavenging guild. Ecological Applications 1:215-225. (Internet)

Stalmaster, M.V. 1976 Winter ecology and effects of human activity on bald eagles in the Nooksack River Valley, Washington. MS Thesis, Western Washington State College, Bellingham.

Stalmaster, M.V. 1980. Management strategies for wintering bald eagles in the Pacific Northwest. Proceedings of the Washington Bald Eagle Symposium, pp 49-67.

Stalmaster, M.V. and J.L. Kaiser. 1998. Effects of recreational activity on wintering bald eagles. Wildlife Monographs 137:1-46.

Stalmaster, M.V. and J.L. Kaiser. 1997. Flushing responses of wintering bald eagles to military activity. Journal of Wildlife Management 61:1307-1313.

Stalmaster, M.V. and J.R. Newman. 1978. Behavioral responses of wintering bald eagles to human activity. Journal of Wildlife Management 42:506-513.

Steenhof, K. 1978. Management of Wintering Bald Eagles. FWS/OBS-78/79. U.S. Fish and Wildlife Service, Department of the Interior, Washington D.C.

Steidl, R.J. and R.G. Anthony. 2000. Experimental Effects of Human Activity on Breeding Bald Eagles. Ecological Applications 10(1), pp. 258-268.

Therres, G.D., M.A. Byrd and D.S. Bradshaw. 1993. Effects of development on nesting bald eagles: case studies from Chesapeake Bay. Transactions of the North American Wildlife and Natural Resources Conference 58:62-69.

U.S. Fish and Wildlife Service. 1979. Bald Eagle Management Guidelines: Oregon – Washington. Portland. OR.

U.S. Fish and Wildlife Service. 1983. Northern States bald eagle recovery plan. Appendices E, F, and G. U.S. Fish and Wildlife Service, Region 6, Denver, CO.

U.S. Fish and Wildlife Service. 1987. Habitat Management Guidelines for the Bald Eagle in the Southeast Region. U.S Fish and Wildlife Service, Region 4. Atlanta, GA.

U.S. Fish and Wildlife Service. 1993. Bald Eagle Basics. Anchorage, AK.

U.S. Fish and Wildlife Service. 1993. Habitat Management Guidelines for Bald Eagles in Texas. Austin, TX.

U.S. Fish and Wildlife Service and Virginia Department of Game and Inland Fisheries. 2001. Bald Eagle Protection Guidelines for Virginia. Gloucester and Richmond, VA.

Watson, J.W. 1993. Responses of nesting bald eagles to helicopter surveys. Wildlife Society Bulletin 21:171-178.

Watson, J.W. 2004. Responses of nesting bald eagles to experimental pedestrian activity. Journal of Raptor Research 38:295-305.

Wood, P.B. 1999. Bald eagle response to boating activity in northcentral Florida. Journal of Raptor Research 33:97-101.

Wood, P.B., T.C. Edwards Jr. and M.W. Collopy. 1989. Characteristics of bald eagle nesting habitat in Florida. Journal of Wildlife Management 53(2):441-449.

Young, L.S. 1980. A quantitative evaluation of human disturbance impacts on breeding eagle ecology of bald eagles in the San Juan Islands, Washington. Washington Department of Game, Olympia.

United States Department of the Interior

FISH AND WILDLIFE SERVICE
Mountain-Prairie Region

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MAY 30 2017

Mr. Brian Ferebee, Regional Forester
United States Forest Service
1617 Cole Boulevard, Building 17
Lakewood, Colorado 80401

Dear Mr. Ferebee:

Thank you for visiting with me on May 16, 2017, regarding concerns related to black-tailed prairie dog population expansion at Thunder Basin National Grasslands (TBNG) in northeastern Wyoming.

The U.S. Fish and Wildlife Service (Service) appreciates the Forest Service's conservation efforts for many wildlife species on these unique lands. The TBNG is one of the few large grassland properties in federal ownership with extensive black-tailed prairie dog populations. Prairie dog concentrations as they exist at TBNG are exceedingly rare and are a haven for golden and bald eagles, other raptors, as well as mountain plovers, burrowing owls, swift fox, and other species of conservation concern. Of particular interest, TBNG is a site that has high potential to contribute to the recovery of the endangered black-footed ferret (ferret). While there are currently no immediate plans to reintroduce the ferret at TBNG, it may well be the best existing site across the species' range in 12 western states, Mexico, and Canada that could significantly contribute to its recovery at the present time.

I understand that your consideration of various stakeholder interests at TBNG, as well as current vegetation and drought conditions, may prompt a revision of the current TBNG Grassland Plan to address reduction of prairie dog populations while still potentially contributing to migratory bird conservation and endangered species recovery. I look forward to providing Service input regarding how compromise might be achieved among all interests and still allow the TBNG to contribute to the Forest Service's responsibilities.

In the short term, however, I feel compelled to advise you of the Service's significant concerns regarding the use of anti-coagulant toxicants for prairie dog control including, but not limited to, brand names Rozol and Kaput. I understand that these products have been approved for use by the Environmental Protection Agency and by some State Government entities; however, I have attached references with summary highlighted concerns of various agencies and other parties related to migratory birds as well as ferrets. In particular, the Service's experience is that the product label requirements are inadequate to limit secondary poisoning of non-target animals and that full label instruction compliance may be limited in practice. Moreover, the use of these products is more expensive and is no more efficient than the use of other products.

You will note in some of the enclosed references that the secondary poisoning of federally protected species continues to occur where anti-coagulant toxicants are used for prairie dog control. While the Service recognizes the need for prairie dog control at TBNG, I urge you to consider less environmentally harmful products in any revised management actions.

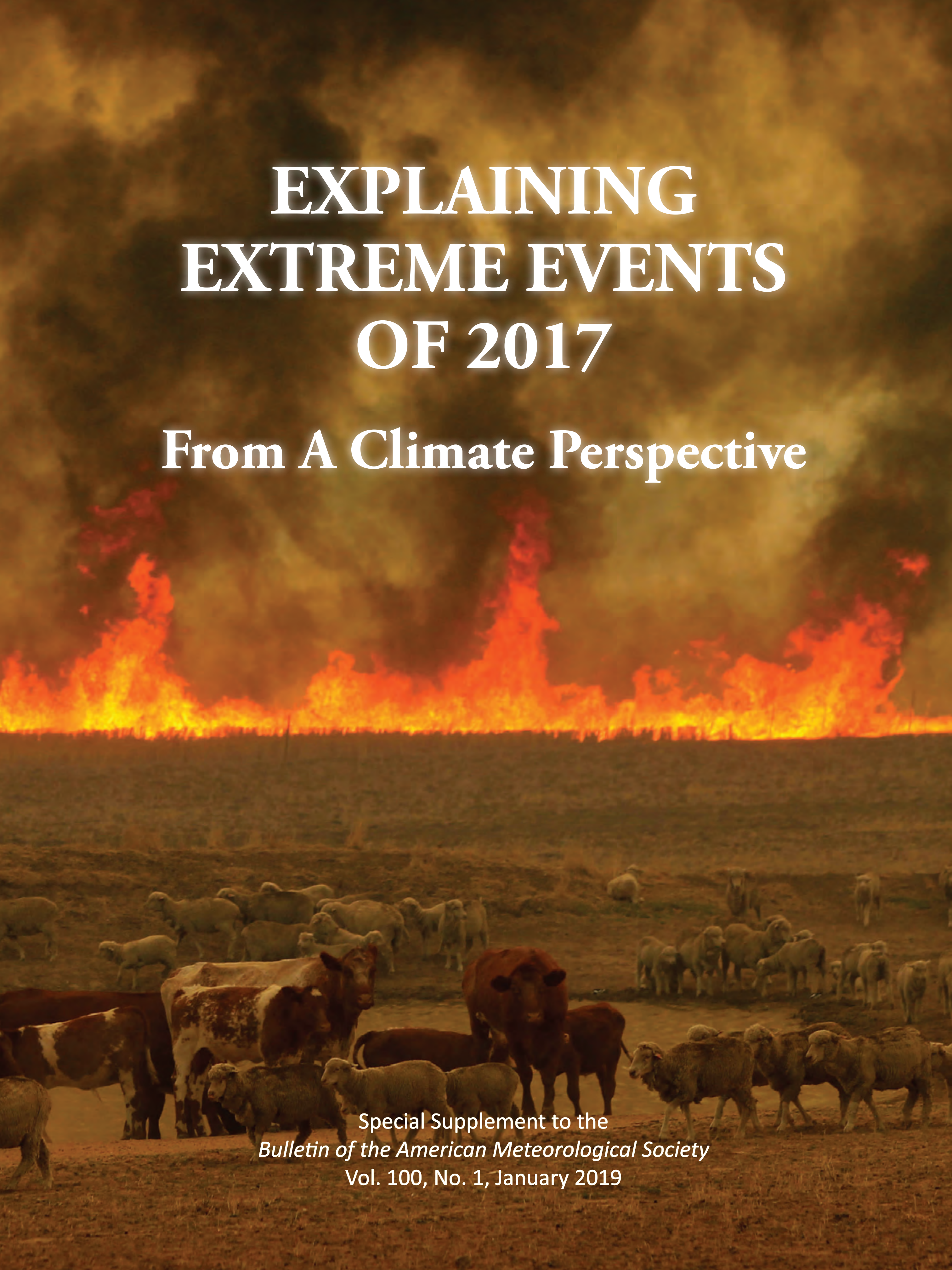
As mentioned above, I will reach out again to share Service perspectives about TBNG Grassland Plan changes. Thank you for your consideration of our joint wildlife conservation interests. If you have any questions concerning this matter, please contact Michael Thabault, Assistant Regional Director for Ecological Services, at (303) 236-4210.

Sincerely,

Noreen E. Walsh

Regional Director

Enclosures (8)



EXPLAINING EXTREME EVENTS OF 2017

From A Climate Perspective

Special Supplement to the
Bulletin of the American Meteorological Society
Vol. 100, No. 1, January 2019

EXPLAINING EXTREME EVENTS OF 2017 FROM A CLIMATE PERSPECTIVE

Editors

Stephanie C. Herring, Nikolaos Christidis, Andrew Hoell,
Martin P. Hoerling, and Peter A. Stott

Special Supplement to the

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COVER CREDIT:

©Dean Sewell/Fairfax Syndication—Sir Ivan Bushfire, February 2017. A bushfire that started near Leadvill, east of Duneedoo in the New South Wales (NSW) Central tablelands, ripped through bush and grasslands in a day that NSW fire authorities classified as catastrophic. Sheep and cattle maneuver around a dam to avoid a fast running bushfire as the fire front moved east. Photograph by Dean Sewell/Oculi.

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TABLE OF CONTENTS

ATTRIBUTION OF THE 2017 NORTHERN HIGH PLAINS DROUGHT

Hailan Wang, Siegfried D. Schubert, Randal D. Koster, and Yehui Chang

The 2017 northern High Plains precipitation deficits were largely the result of internal atmospheric variability. Global warming may have exacerbated the dry condition by producing surface warming and increasing the probability of heat waves there.

INTRODUCTION. The northern High Plains, particularly much of Montana and the Dakotas, had extreme to exceptional drought conditions develop during the summer of 2017. When the months of May, June, and July are combined, the year 2017 received 60% of normal precipitation and is ranked as the second driest (only after 1936) of the period 1901–2017 (Fig. 1a; see also Fig. ES1a in the online supplemental material). It also had anomalously warm temperatures relative to the 1901–2017 record (Figs. 1b and ES1b). The exceptional dryness combined with the unusual heat over central and eastern Montana resulted in a rapidly declining Palmer Severity Drought Index, which, although of short duration, reached extreme drought levels comparable to those of historical droughts (e.g., during the 1930s). The occurrence of the drought over Montana and the Dakotas, an important spring wheat–growing region in the country, during the crop growing season caused agricultural losses of $2.5 billion and contributed to one of Montana's worst wildfire seasons on record (NOAA/NCEI 2018).

AFFILIATIONS: Wang—Science Systems and Applications, Inc., Lanham, Maryland; Schubert—Global Modeling and Assimilation Office, NASA Goddard Space Flight Center, Greenbelt, and Science Systems and Applications, Inc., Lanham, Maryland; Koster— Global Modeling and Assimilation Office, NASA Goddard Space Flight Center, Greenbelt, Maryland; Chang— Global Modeling and Assimilation Office, NASA Goddard Space Flight Center, Greenbelt, and Morgan State University, Baltimore, Maryland
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This study investigates the causes of the 2017 northern High Plains drought, particularly the roles of the 2017 sea surface temperature (SST) anomalies and atmospheric internal variability. It also assesses the impact of the post-1901 long-term warming trend on the frequency of drought occurrence in the area.

DATA AND METHODS. This study makes use of various observational datasets, including the NOAA Extended Reconstructed SST (ERSST) version 5 (Huang et al. 2017), the Global Precipitation Climatology Project (GPCP) precipitation (Adler et al. 2003), and the Global Precipitation Climatology Centre (GPCC) land precipitation (Schneider et al. 2014). Data from the NASA Modern-Era Retrospective Analysis for Research and Applications, version 2 (MERRA-2; Gelaro et al. 2017) are used as well.

The study also utilizes two sets of Atmospheric Model Intercomparison Project (AMIP) simulations performed with the NASA Goddard Earth Observing System Model, version 5 (GEOS-5) atmospheric general circulation model (AGCM) (Rienecker et al. 2008; Molod et al. 2012), forced with observed monthly SST, sea ice, and time-varying greenhouse gases (Schubert et al. 2014). The first set is used to investigate the impacts of the 2017 SST anomalies and atmospheric internal variability on the drought event in the context of current climate; here, a GEOS-5 (tag: Ganymed 4.0) AMIP simulation covering 1980–2014 provided a climatology, and a 90-member ensemble of AMIP simulations performed for 2017 provided a robust estimate of model atmospheric internal variability during that year. These AMIP runs employed a tendency bias correction to the basic state variables (estimated from the time-mean MERRA-2 analysis increments) that removes much of the model bias in the mean climate and its variability (Wang et al. 2018). The second set of AMIP simulations consists of 12 archived long-

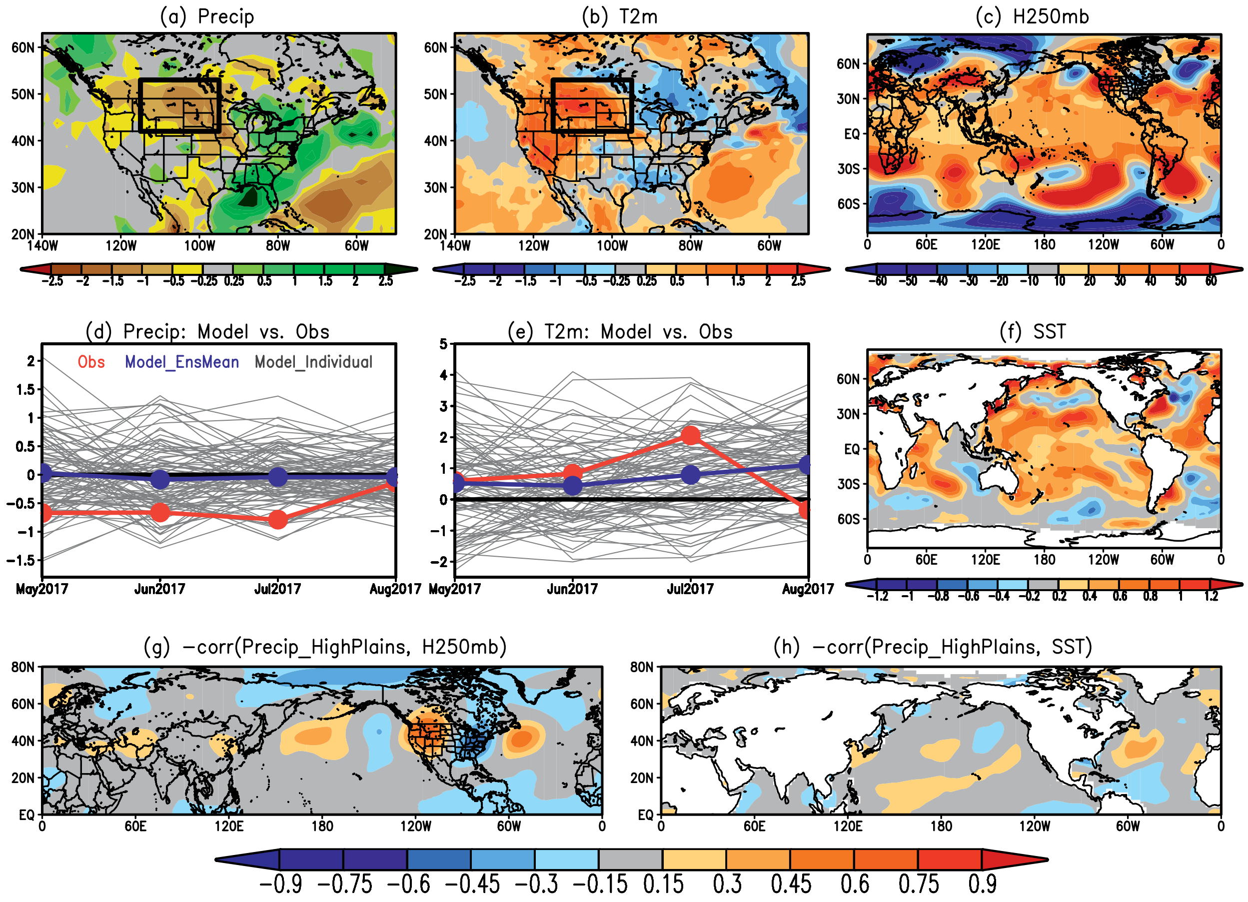

Fig. 1. The observed May–July 2017 anomalies in (a) precipitation from GPCP (mm day^{-1}), (b) surface air temperature anomalies (K) from MERRA-2, and (c) 250-mb geopotential height (m) from MERRA-2. (d) The comparison between observations (GPCP), the 90 GEOS-5 AMIP members, and their ensemble mean for monthly precipitation anomalies (mm day^{-1}) averaged over the 2017 drought region (245°–265°E, 42°–53°N) for May–August 2017. (e) As in (d), but for surface air temperature (K). (f) As in (a), but for NOAA SST (unit: K). (g) The temporal correlation between GPCP precipitation averaged over the 2017 drought region and MERRA-2 250-mb geopotential height for May–July averages for 1980–2017; (h) as in (g), but for NOAA SST. The above anomalies are obtained as deviations from their climatology over the period 1980–2014. The 2017 drought region is indicated using a black box in (a) and (b).

term simulations (1901–2014) performed with an earlier version of the GEOS-5 AGCM (tag: Fortuna 2.4) (Schubert et al. 2014); it is used to assess the effects of historical warming. The dependence of the attribution analysis on climatologies used and the model dependence of our assessments are examined by also considering long-term NCAR CAM5 AMIP simulations (1901–2017; 40 members).[1] Since the precipitation deficit and surface warming anomalies in the northern High Plains mainly occurred during May–July 2017, our analyses focus on the average of these three months.

RESULTS. Figure 1 examines the 2017 northern High Plains drought relative to the 1980–2014 climatology. The observed May–July averaged precipitation deficits occurred over the northern Plains and southern Canadian prairies (Fig. 1a). Meanwhile, much of the western half of the United States experienced warmer-than-normal temperatures, with peak warming over Montana, the Dakotas, and the southwestern United States (Fig. 1b). The accompanying geopotential height anomalies in the upper troposphere consisted of widespread warming in the tropics and much of the midlatitudes, a reflection of global SST warming trends during recent decades (e.g., Schubert et al. 2014), as well as a zonal wave train that spans the North Pacific and North America, with an anomalous barotropic high centered over the northwestern United States (Fig. 1c). The high anomaly, which

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[1] The long-term NCAR CAM5 AMIP simulations are produced by the NOAA ESRL Attribution and Predictability Assessments Team and are made available at the NOAA/ESRL/PSD Climate Data Repository (www.esrl.noaa.gov/psd/repository/alias/facts).

persisted throughout much of May–July 2017 (not shown), contributed to the local surface warming by suppressing the formation of local convection and clouds and leading to increased solar radiation at the surface. Meanwhile, the northerly anomaly at its east flank in the lower troposphere weakened the Great Plains low-level jet (LLJ) and inhibited northward atmospheric moisture transport by the jet, leading to precipitation deficits in the northern High Plains.

To investigate the physical processes for the 2017 drought event, we compared anomalies from the first set of GEOS-5 AMIP simulations with observations (Figs. 1d,e). Here the model ensemble average highlights the SST-forced signal, whereas the spread among the ensemble members reflects the unforced variability generated by processes internal to the atmosphere. The observed SST anomalies show warming over much of the tropical and subtropical oceans (Fig. 1f). When forced with these SST anomalies, the ensemble mean of the GEOS-5 AGCM simulations shows little change in precipitation but a notable surface warming in the northern High Plains. The observed anomalies fall within the fairly large model ensemble spread, with the observed precipitation anomalies falling near the dry edge of the spread. Only three ensemble members (out of 90) show persistent dry and warm responses similar to the observations. These results suggest that the 2017 warm SST anomalies encouraged surface warming in the northern High Plains, while atmospheric internal variability explains much of the precipitation deficits. A parallel analysis using the CAM5 AMIP simulations (1901–2017) shows that the above conclusion is not changed when viewed in the context of the century long (1901–2014) climate (cf. Figs. 1d,e with Figs. ES1c–f); furthermore, it appears that much of the 2017 SST-forced surface warming in the northern High Plains is a response to the long-term SST warming trend (see the online supplemental information). Figure 1g shows that the year-to-year variation of summertime precipitation in the northern High Plains is typically associated with a zonal wave train (of roughly wavenumber 5) in the NH midlatitudes; its connection to SST is weak overall (Fig. 1h). Such a wave train resembles the leading patterns of upper-level circulation variability within the jet waveguide during boreal summer (Ding and Wang 2005; Schubert et al. 2011). The nature of the drought-inducing atmospheric internal variability is yet unclear and needs further research.

In our second analysis, we investigate the effect of historical warming on the occurrence of extreme dry events in the northern High Plains by comparing two time periods from the long-term GEOS-5 AMIP simulations: 1901–70 and 1980–2014, with the latter period coinciding with the start of a period of enhanced global warming. The May–July mean SST differences between the two periods (Fig. 2a) reflects the long-term warming trend over the twentieth century, as evidenced by its resemblance to the SST warming trend pattern that is obtained as the leading rotated empirical orthogonal function (REOF) of annual mean SST over 1901–2004 (Schubert et al. 2009). Most of the effects of decadal to multidecadal oscillations (e.g., the Pacific decadal oscillation and Atlantic multidecadal oscillation) are thus averaged out in the two periods. Relative to the early period, the ensemble mean upper-level geopotential height in the latter period (Fig. 2b) increases nearly everywhere, with local maxima occurring over the northwestern United States and the Bering Sea, presumably forced by the long-term SST changes (Fig. 2a). In fact, such atmospheric circulation changes resemble the responses of this model and four other AGCMs participating in the U.S. CLIVAR drought working group (Schubert et al. 2009) to the above-mentioned SST warming trend pattern (not shown), suggesting that the circulation changes in Fig. 2b are a robust dynamical response to the warming trend pattern.

We investigate the effects of historical global warming on the occurrence of drought extremes in the northern High Plains by comparing the probability density functions (PDFs) of drought-related variables in the two periods. The precipitation PDFs in the northern High Plains for the two periods are very similar (Fig. 2c), consistent with indications from GPCC observations (not shown). There are, however, clear indications of an increased probability of warmer surface air temperature in the recent period (Fig. 2d), which leads to a modest increase in the risk for drier soil (Fig. 2e). The AMIP simulations thus suggest that agricultural droughts (soil moisture deficits) are more probable during recent times. Evapotranspiration shows a slight net decrease (not shown), a reflection of the slight decrease in precipitation. There are also clear indications of an increased probability of a moister atmosphere over the central United States (Fig. 2f) and increased eddy height anomalies over the northwestern United States (Fig. 2g). While the moister atmosphere tends to increase atmospheric moisture transport to the northern High Plains and thus precipitation there, the increased eddy height anomalies tend to reduce this precipitation by inducing subsidence in the northern High Plains as well as by weakening the Great Plains LLJ. In other words, the modest

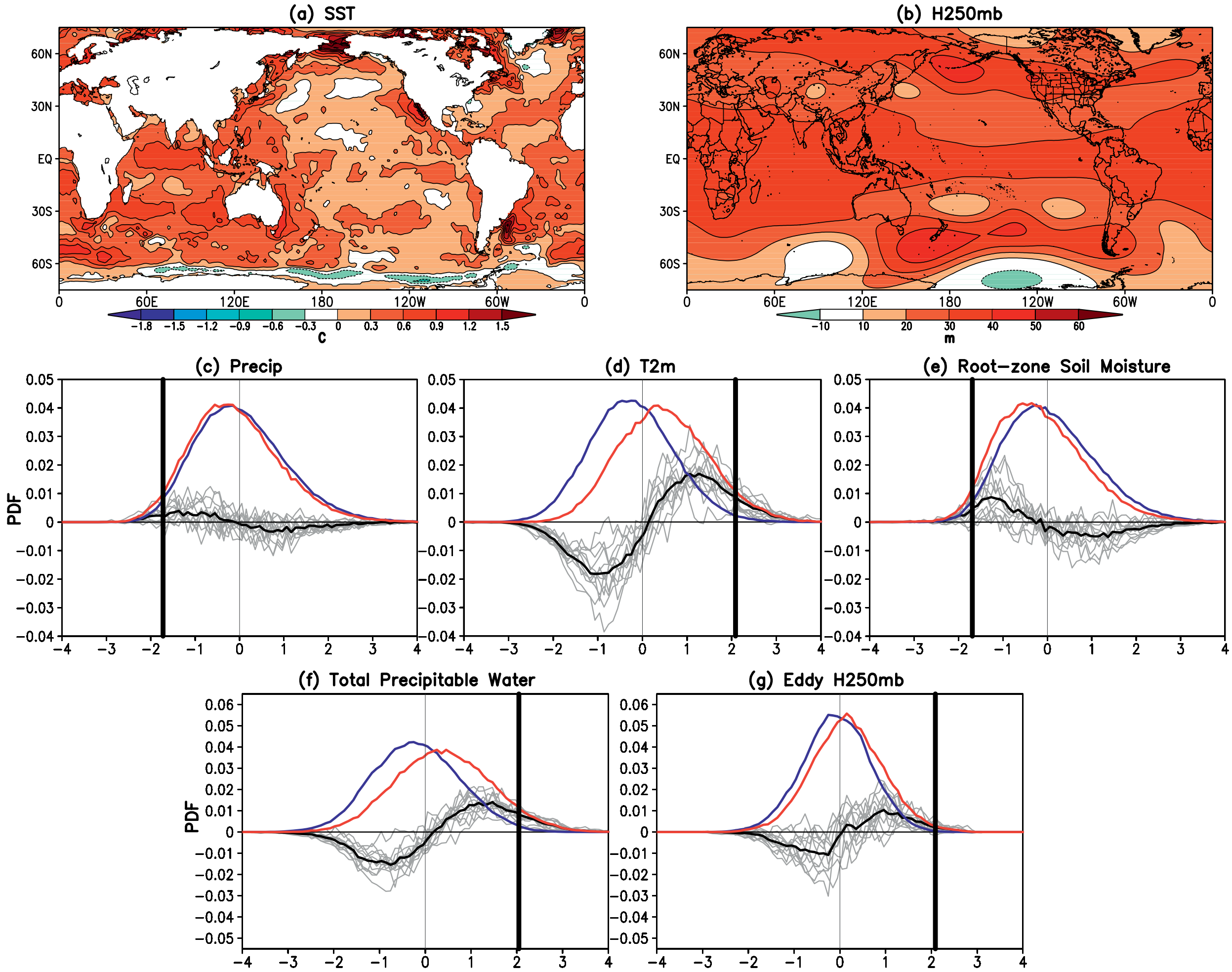

Fig. 2. (a) The observed climatology difference of May–July SST between the periods 1901–70 and 1980–2014. (b) As in (a), but for the 250-mb geopotential height in the GEOS-5 AMIP ensemble mean simulation. (c) The PDF of precipitation over the 2017 drought region (245°–265°E; 42°–53°N) for the periods 1901–70 (blue) and 1980–2014 (red) using the 12 GEOS-5 AMIP simulations combined, the PDF difference between the two time periods using the 12 AMIP simulations combined (black), and each of the 12 AMIP simulations (gray). (d),(e) As in (c), but respectively for surface air temperature and root-zone soil moisture (moisture in the top meter of soil, as determined from soil moisture prognostic states in the GEOS-5 land surface model). (f),(g) As in (c), but respectively for total column water vapor over the central United States (245°–265°E; 30°–45°N) and the 250-mb zonally asymmetric geopotential height over the northwestern United States (232°–257°E, 35°–52°N). The critical values of 2.5% associated with dry conditions based on the distribution over 1901–2014 are shown using thick black vertical lines. [Note that the PDF analysis in (c)–(g) uses data at all grid points in the selected domains. Anomalies used in the PDF analysis are normalized deviations from the climatology over the period 1901–2014.]

change in the precipitation PDF (Fig. 2c) appears to reflect counteracting impacts of the thermodynamic and dynamical processes. A parallel analysis using the CAM5 simulations (Fig. ES2) produces results similar to those based on the GEOS-5 model (Fig. 2), supporting that our findings are not model dependent. We also emphasize that the impact of dynamical processes examined here reflects the model's response to the observed SST changes that occurred during the period of 1901–2014. As such, the dynamical impact may be different in models (e.g., CMIP5 historical simulations) that simulate mean SST changes different from the observed.

CONCLUSIONS. The 2017 northern High Plains drought and associated heat waves were induced in part by a positive height anomaly that persisted over the northwestern United States and the northern High Plains throughout much of May–July 2017. Our model results show that while the observed 2017 SST anomalies provided a predilection for drought by inducing surface warming, internal atmospheric variability accounts for the extreme precipitation deficits.

An assessment of the role of historical global warming shows no appreciable increase in the risk of precipitation deficits but an increased risk of heat waves in the northern High Plains. In fact, a substantial fraction of the 2017 SST-forced surface warming appears to be a response to the global warming signal. The small change in the probability of precipitation deficits over the historical period appears to reflect counteracting effects of thermodynamic processes (increased atmospheric moisture over the United States) and dynamical processes (increased eddy height over the northwestern United States). The increased risk for heat waves may have increased the likelihood of agricultural (soil moisture) drought in the region, and contributed to exacerbating the 2017 drought.

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REFERENCES

Adler, R. F., and Coauthors, 2003: The version-2 Global Precipitation Climatology Project (GPCP) monthly precipitation analysis (1979–present). *J. Hydrometeor.*, **4**, 1147–1167, https://doi.org/10.1175/1525-7541(2003)004<1147:TVGPCP>2.0.CO;2.

Ding, Q., and B. Wang, 2005: Circumglobal teleconnection in the Northern Hemisphere summer. *J. Climate*, **18**, 3483–3505, https://doi.org/10.1175/JCLI3473.1.

Gelaro, R., and Coauthors, 2017: The Modern-Era Retrospective Analysis for Research and Applications, version 2 (MERRA-2). *J. Climate*, **30**, 5419–5454, https://doi.org/10.1175/JCLI-D-16-0758.1.

Huang, B., and Coauthors, 2017: Extended Reconstructed Sea Surface Temperature version 5 (ERSSTv5), Upgrades, validations, and intercomparisons. *J. Climate*, 30, 8179–8205, https://doi.org/10.1175/JCLI-D-16-0836.1.

Molod, A., L. Takacs, M. Suarez, J. Bacmeister, I.-S. Song, and A. Eichmann, 2012. The GEOS-5 atmospheric general circulation model: Mean climate and development from MERRA to Fortuna. NASA Technical Report Series on Global Modeling and Data Assimilation, NASA TM-2012-104606, Vol. 28, 117 pp.

NOAA/NCEI, 2018: Billion-dollar weather and climate disasters. NOAA National Centers for Environmental Information, www.ncdc.noaa.gov/billions/.

Rienecker, M. M., and Coauthors, 2008: The GEOS-5 data assimilation system—Documentation of versions 5.0.1, 5.1.0, and 5.2.0. NASA Tech. Rep. Series on Global Modeling and Data Assimilation, NASA/TM-2007-104606, Vol. 27, 95 pp.

Schneider, U., A. Becker, P. Finger, A. Meyer-Christoffer, M. Ziese, and B. Rudolf, 2014: GPCC's new land surface precipitation climatology based on quality-controlled in situ data and its role in quantifying the global water cycle. *Theor. Appl. Climatol.*, **115**, 15–40, https://doi.org/10.1007/s00704-013-0860-x.

Schubert, S., and Coauthors, 2009: A U.S. CLIVAR project to assess and compare the responses of global climate models to drought-related SST forcing patterns: Overview and results. *J. Climate*, **22**, 5251–5272, https://doi.org/10.1175/2009JCLI3060.1.

——, H. Wang, and M. Suarez, 2011: Warm season subseasonal variability and climate extremes in the Northern Hemisphere: The role of stationary Rossby waves. *J. Climate*, **24**, 4773–4792, https://doi.org/10.1175/JCLI-D-10-05035.1.

——, ——, R. Koster, M. Suarez, and P. Groisman, 2014: Northern Eurasian heat waves and droughts. *J. Climate*, **27**, 3169–3207, https://doi.org/10.1175/JCLI-D-13-00360.1.

Wang, H., S. D. Schubert, Y. Chang, and R. D. Koster, 2018: Subseasonal prediction of warm season drought in North America. *42nd NOAA Climate Diagnostics and Prediction Workshop*, Norman, OK, National Weather Service, www.cpc.ncep.noaa.gov/products/outreach/CDPW42/11-Wang.pdf.