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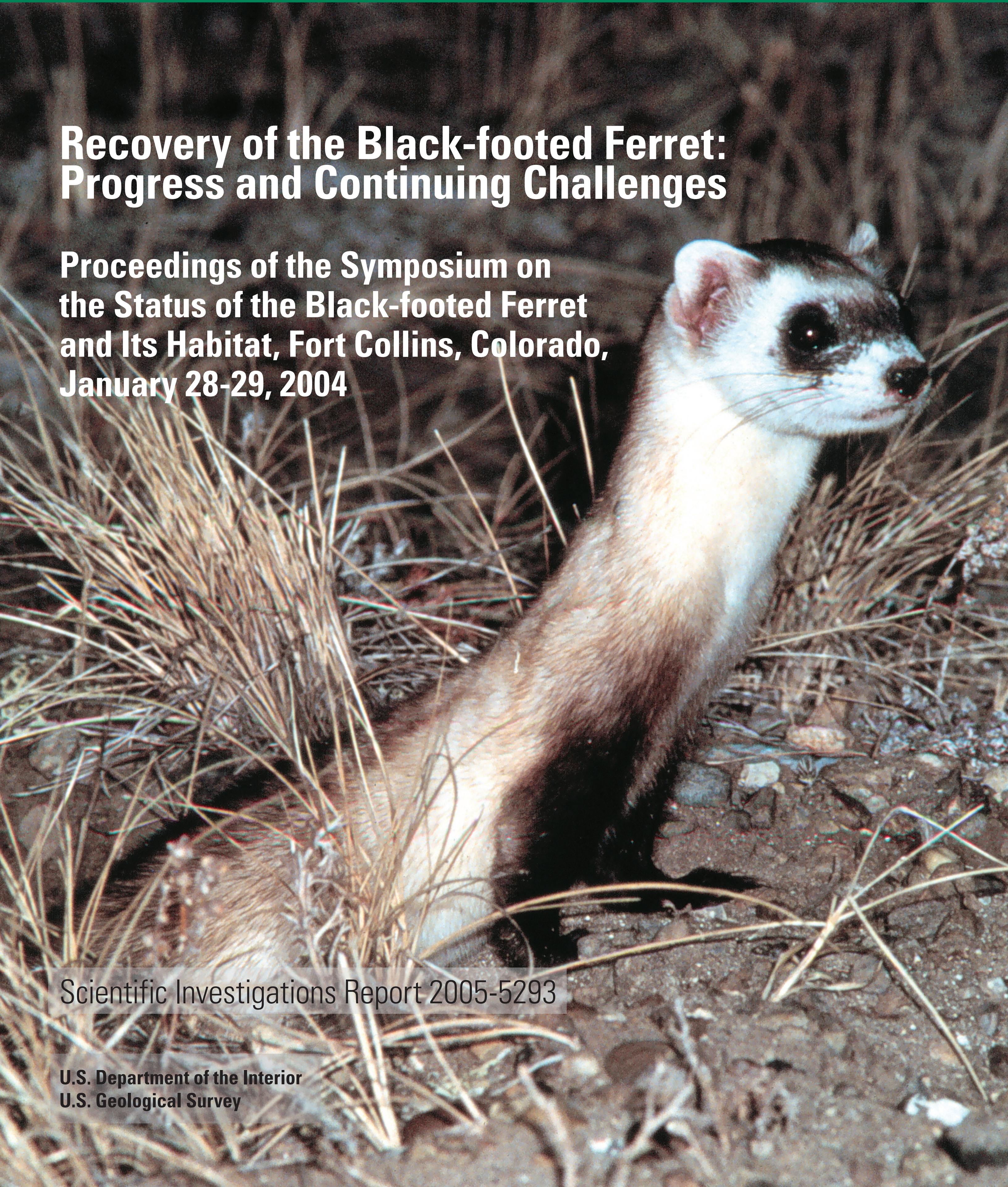

Recovery of the Black-footed Ferret: Progress and Continuing Challenges

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


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Edited by James E. Roelle, Brian J. Miller, Jerry L. Godbey, and Dean E. Biggins

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DIRK KEMPTHORNE, Secretary

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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.

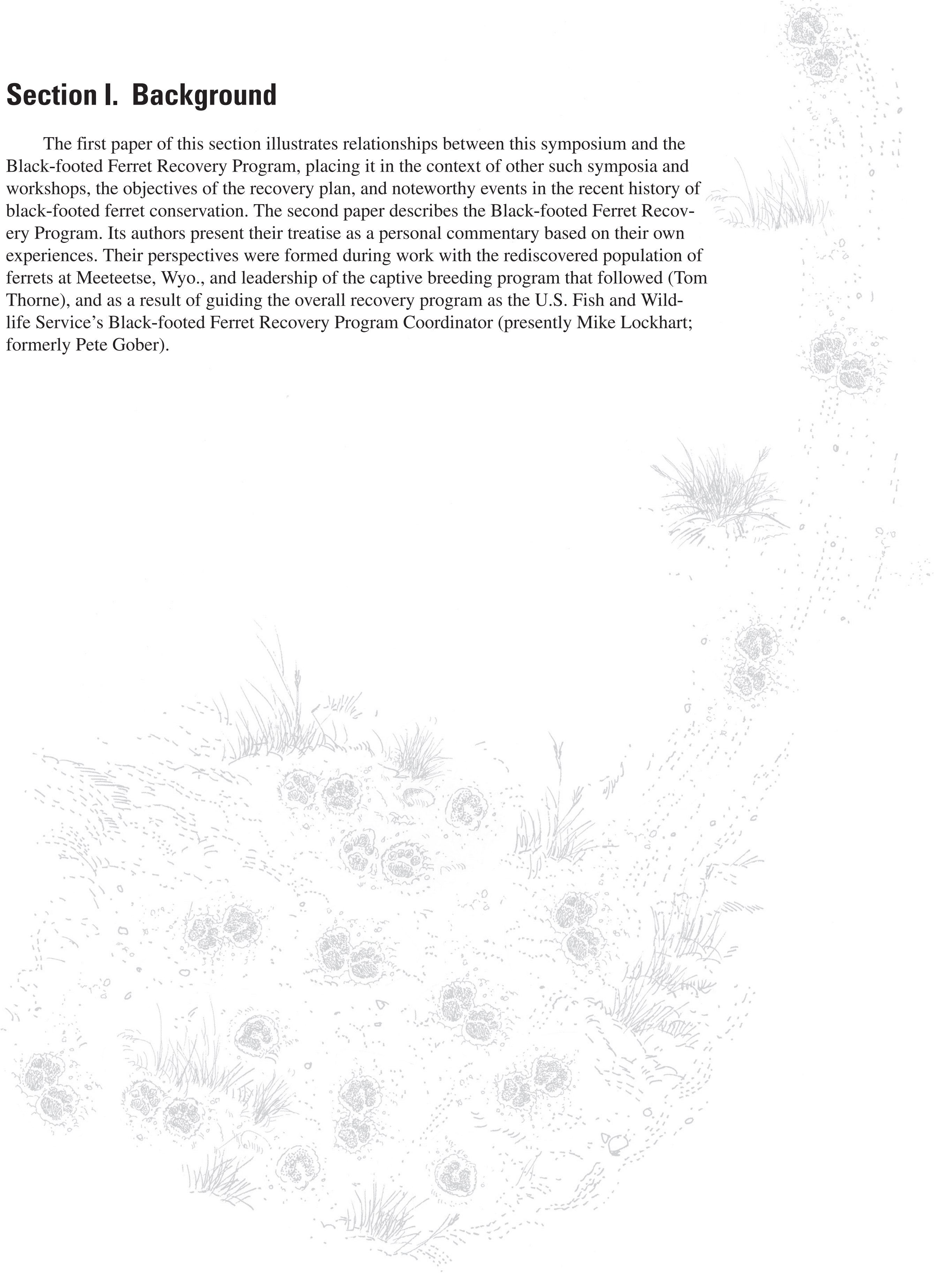
Stan Anderson died at his home in Laramie on September 1, 2005, following an extended illness. Stan started the University of Wyoming Cooperative Fish and Wildlife Research Unit in 1980 and served as a graduate advisor for many biologists who obtained advanced degrees studying various aspects of prairie 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 Branvold
'98

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

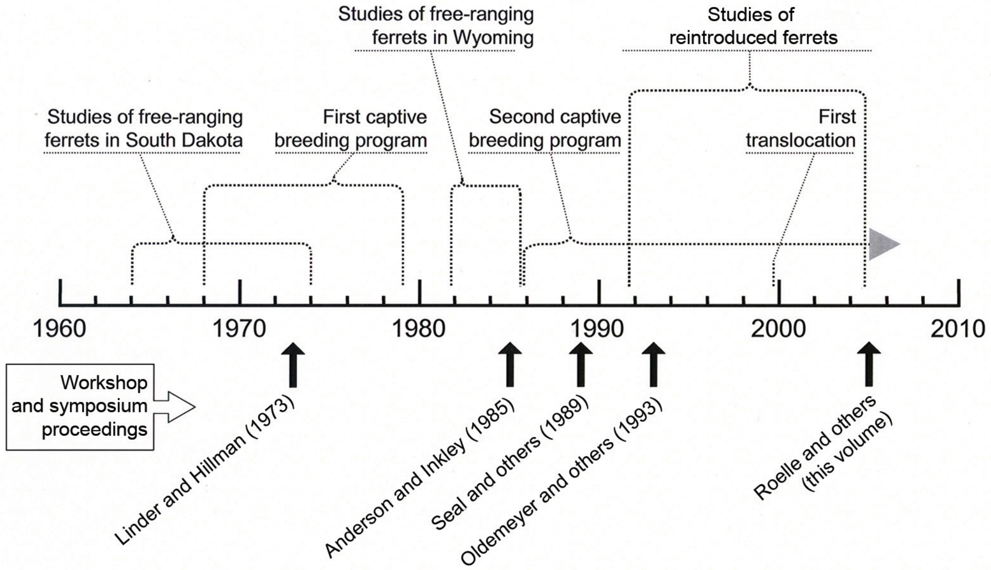


Figure 1. Timeline relating recent symposia and workshops to noteworthy events and periods in black-footed ferret (*Mustela nigripes*) research and recovery.

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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.

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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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[3] U.S. Fish and Wildlife Service, 420 S. Garfield Ave., Suite 400, Pierre, SD 57501.

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.

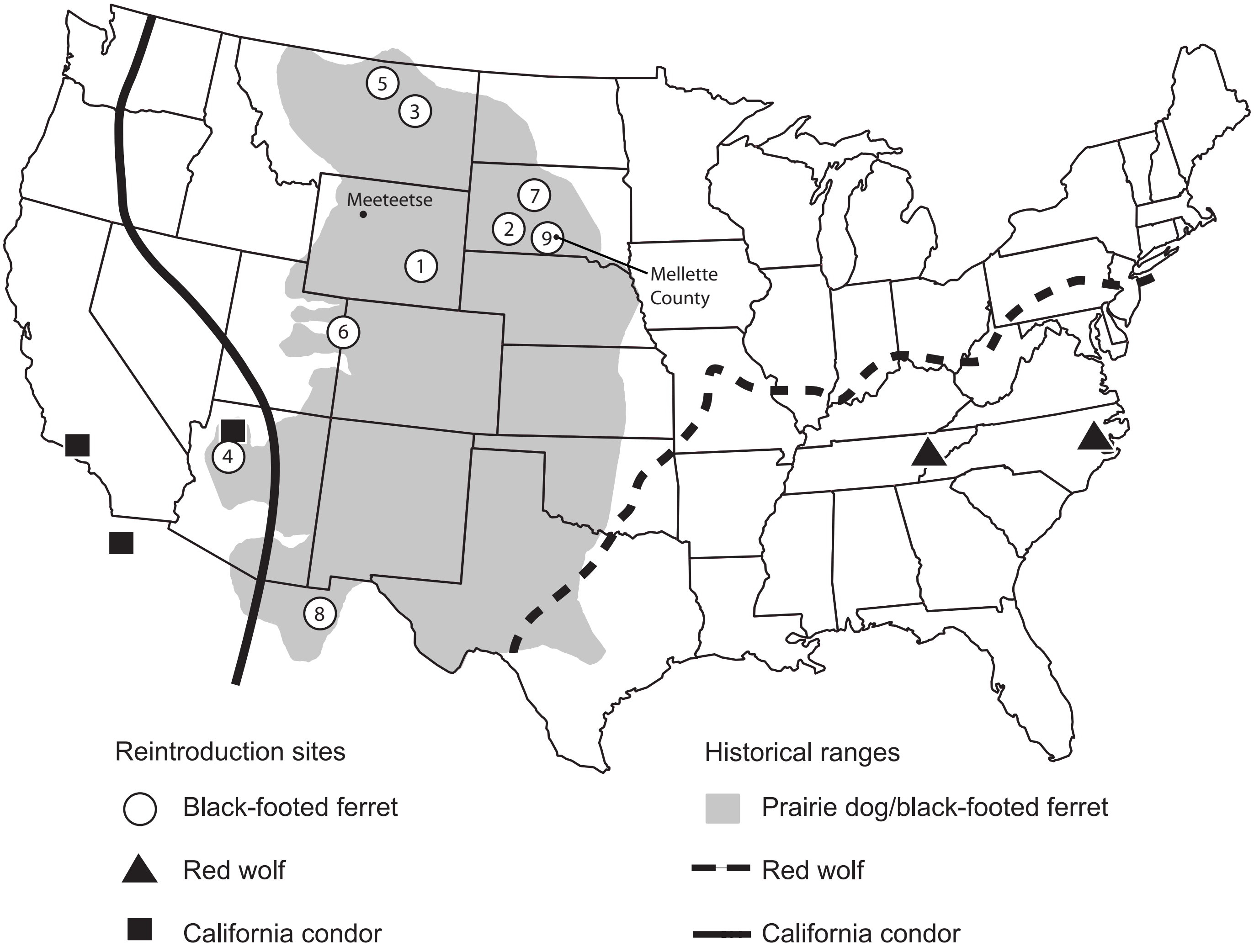

Figure 1. Location of black-footed ferret (*Mustela nigripes*) reintroduction sites overlaid on the collective ranges of three major prairie dog (*Cynomys*) species that are considered their obligate prey. Numbers represent the chronological sequence of ferret reintroductions. Also shown are locations 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.

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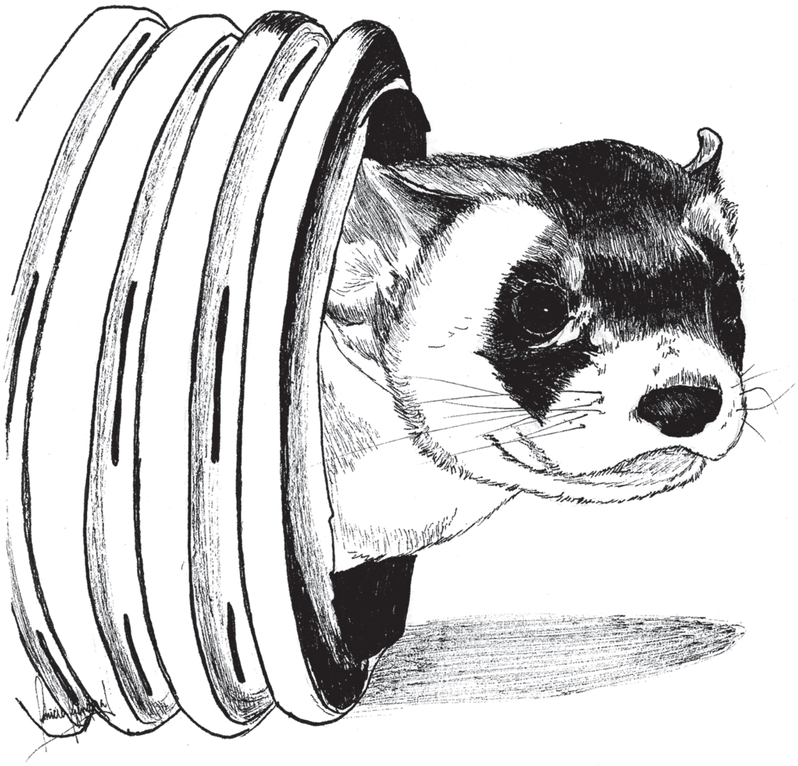
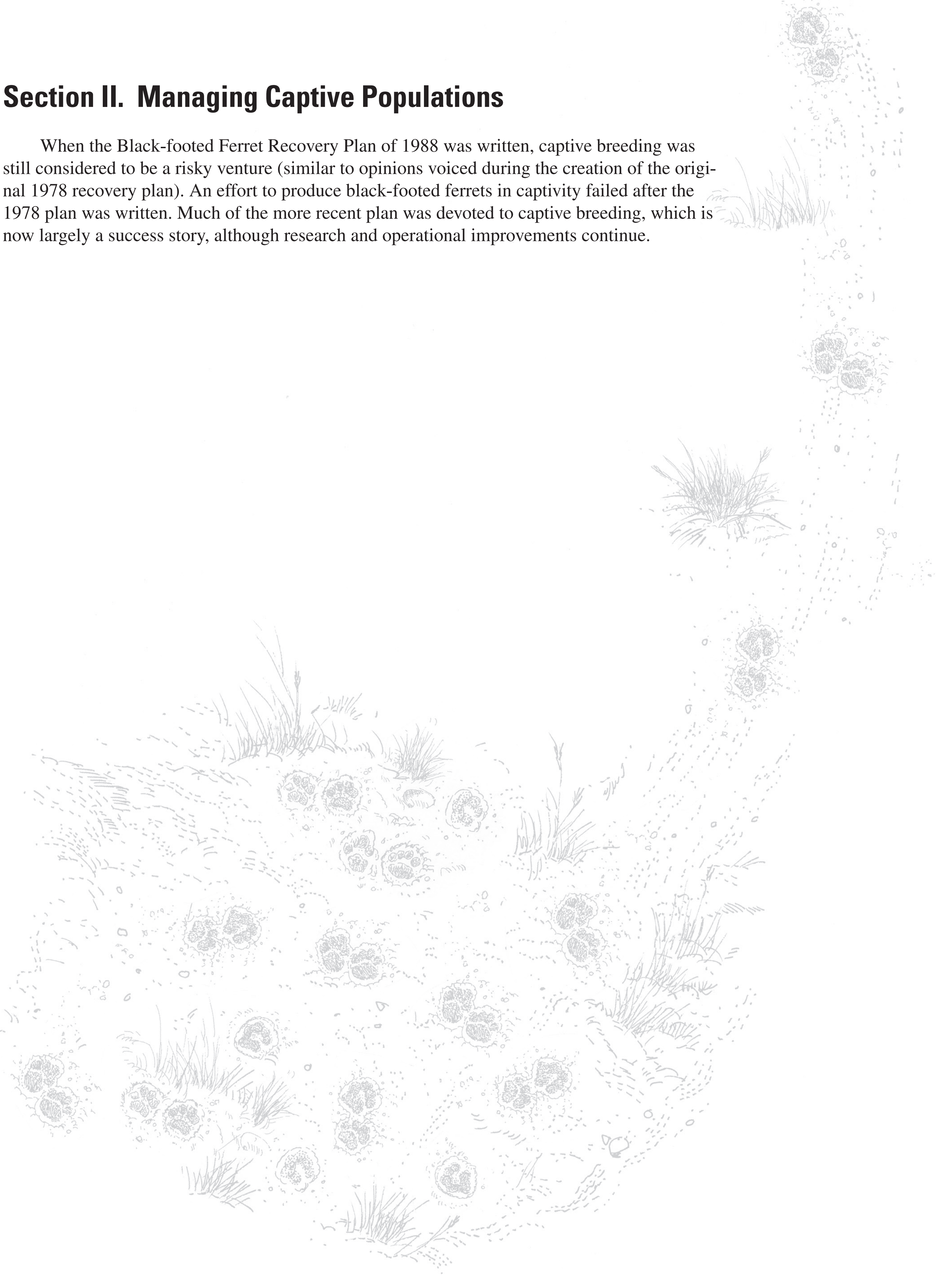
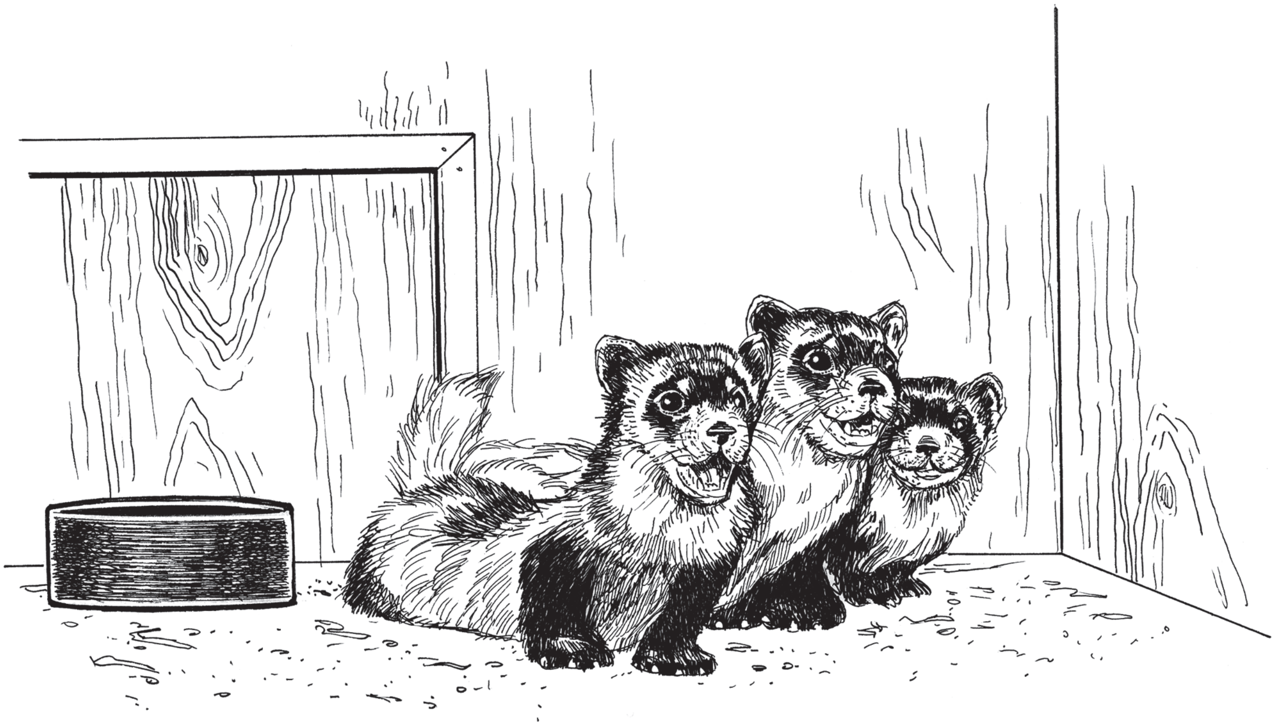


Section II. Managing Captive Populations

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.

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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.

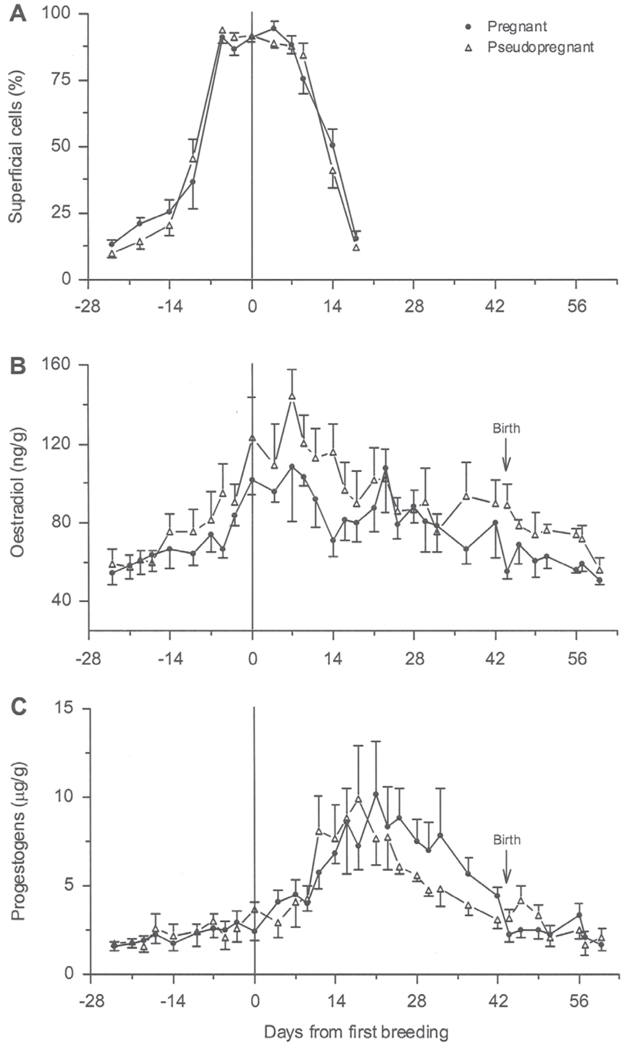

Figure 1. Mean (± SE) percent superficial cells in vaginal lavages (A) and fecal oestradiol (B) and progestogen (C) metabolite concentrations in pregnant (n = 7) and pseudopregnant (n = 9) black-footed ferrets (*Mustela nigripes*). Day 0 is the time of first mating. (From Brown, 1997. Reprinted with 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).

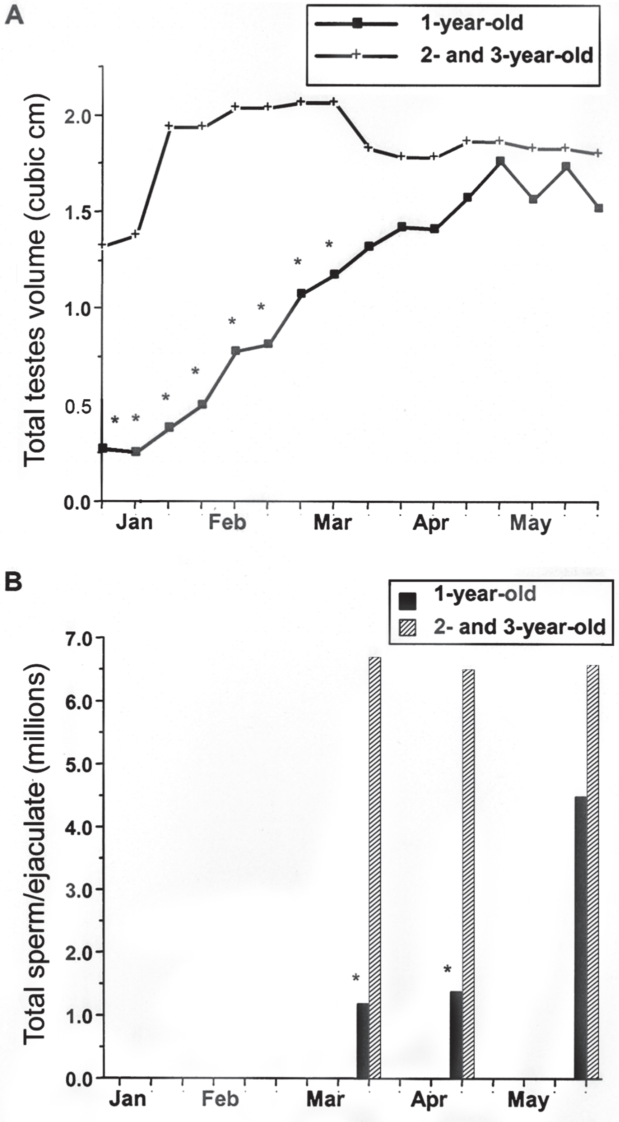

Figure 2. Influence of age on testes development (A) and total sperm/ejaculate (B) in 1-year-old versus 2- and 3-year-old male black-footed ferrets (*Mustela nigripes*). Asterisks indicate differences ($P < 0.05$) between age groups within a month.

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.

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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

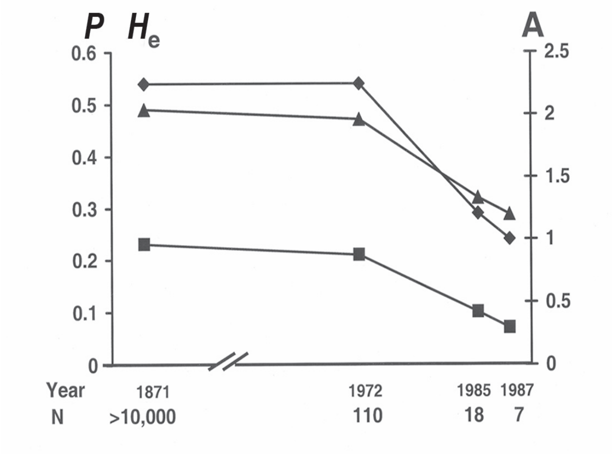

Figure 1. A timeline of genetic diversity in the black-footed ferret (*Mustela nigripes*). A, the average number of alleles per locus (triangle); H_e, expected heterozygosity (diamond); and P, the proportion of polymorphic loci (square) were at their highest values in 1871. In 1972 only two populations 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.)

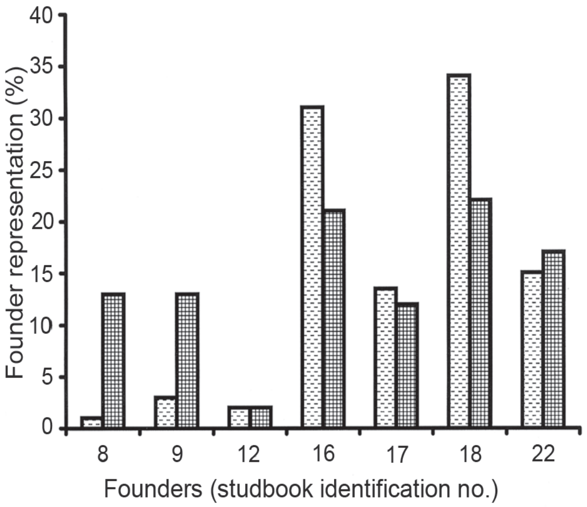

Figure 2. Founder representation in the first generation of captive breeding (i.e., all the direct descendants) (dotted bars) and in 1999, after 14 years of captive breeding (cross-hatched bars) of black-footed ferrets (*Mustela nigripes*). Only founders with genes represented in the extant population 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	$H_e \pm 2$ 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.

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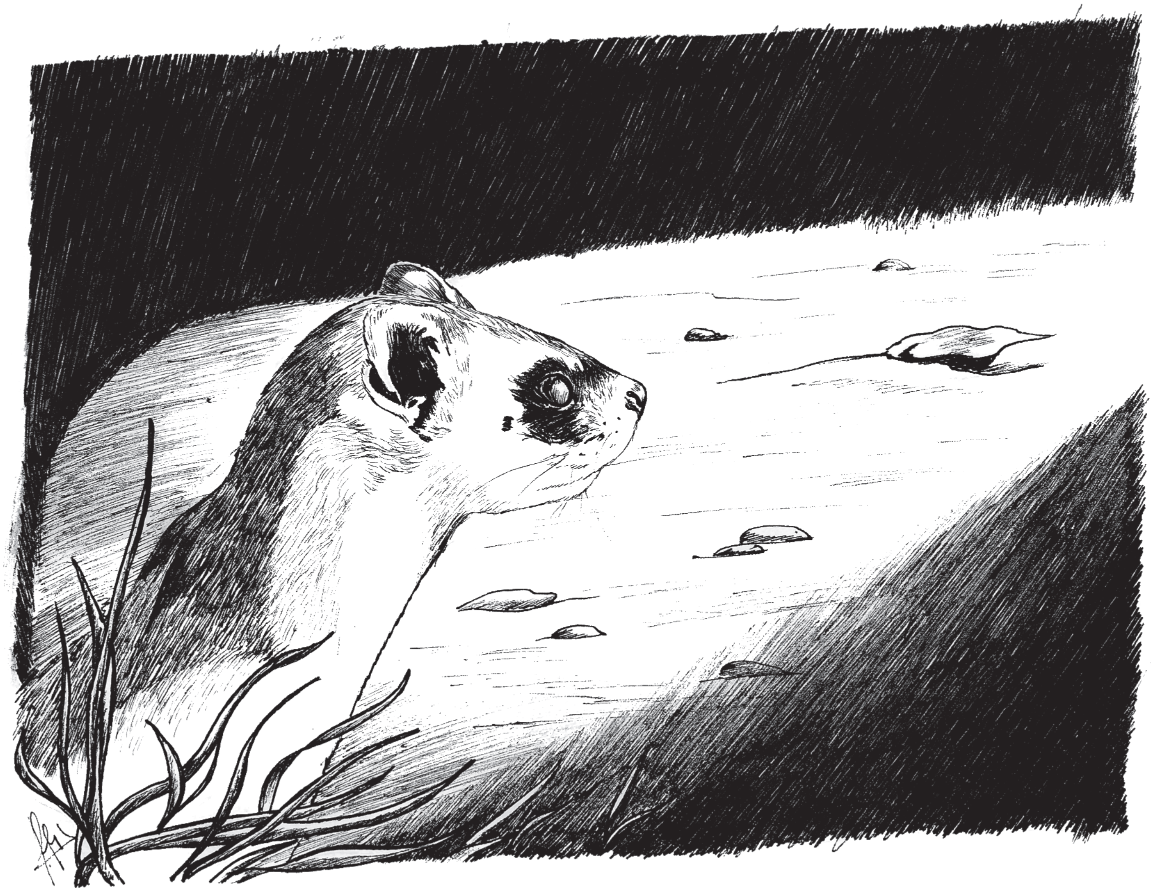
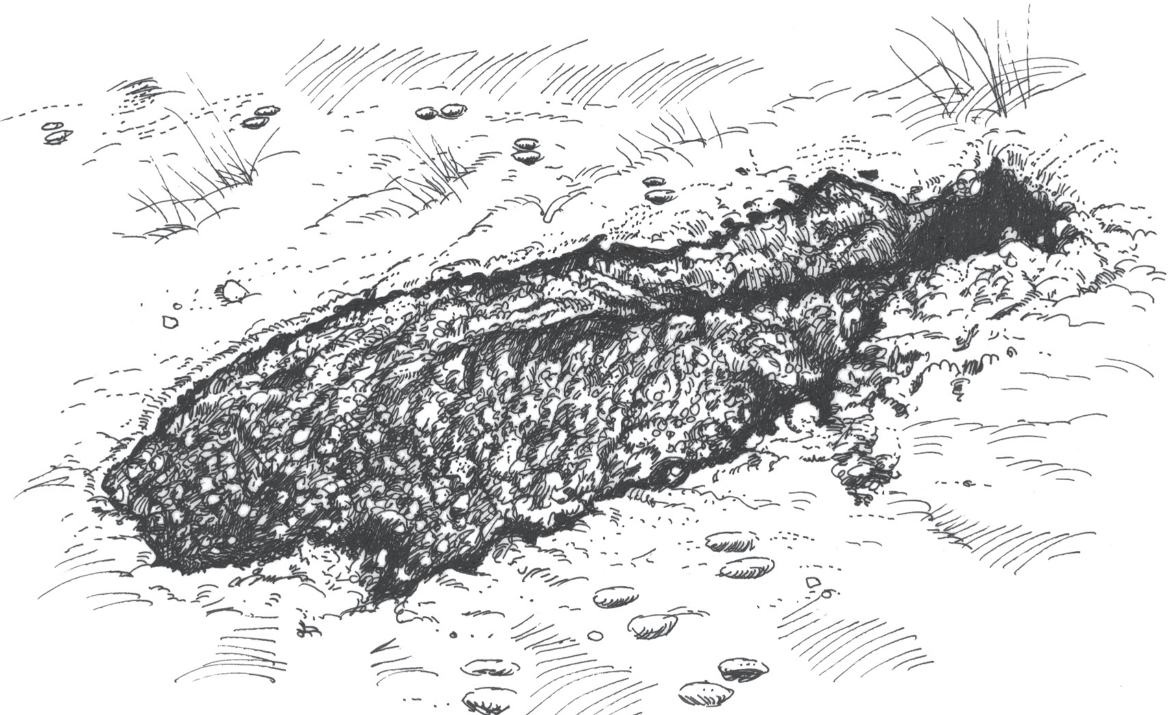


Section III. Searching for Wild Black-footed Ferrets

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).

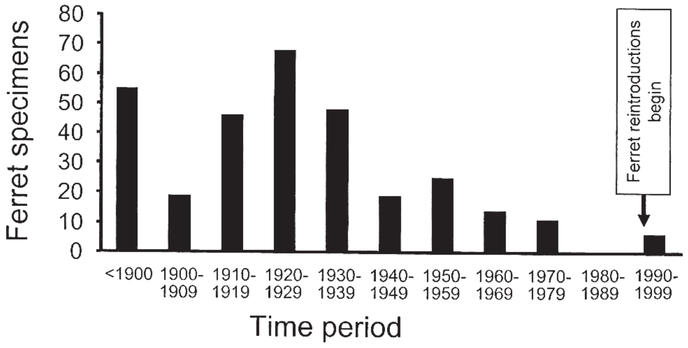

Figure 1. Number of black-footed ferret (*Mustela nigripes*) specimens collected by decade from Anderson and others (1986) and Clark (1989), including the decade after ferret reintroductions.

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.

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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

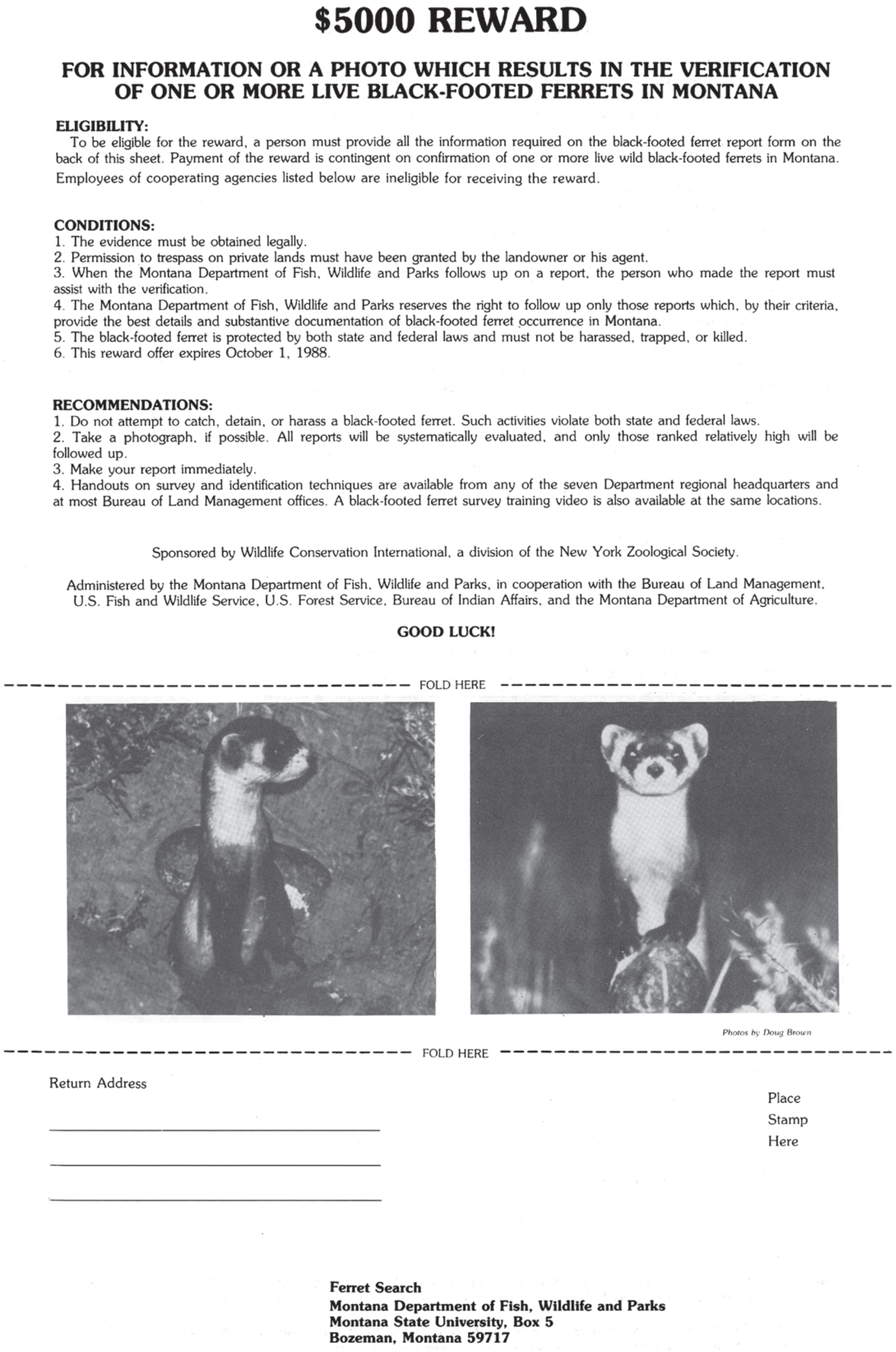
REWARD CONDITIONS: The ferret is an endangered species and is protected by very stringent federal and state laws. The reward WILL NOT be paid for any ferret caught in traps or killed by the finder. The reward will be given to the FIRST person providing information leading to the discovery and verification 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

____

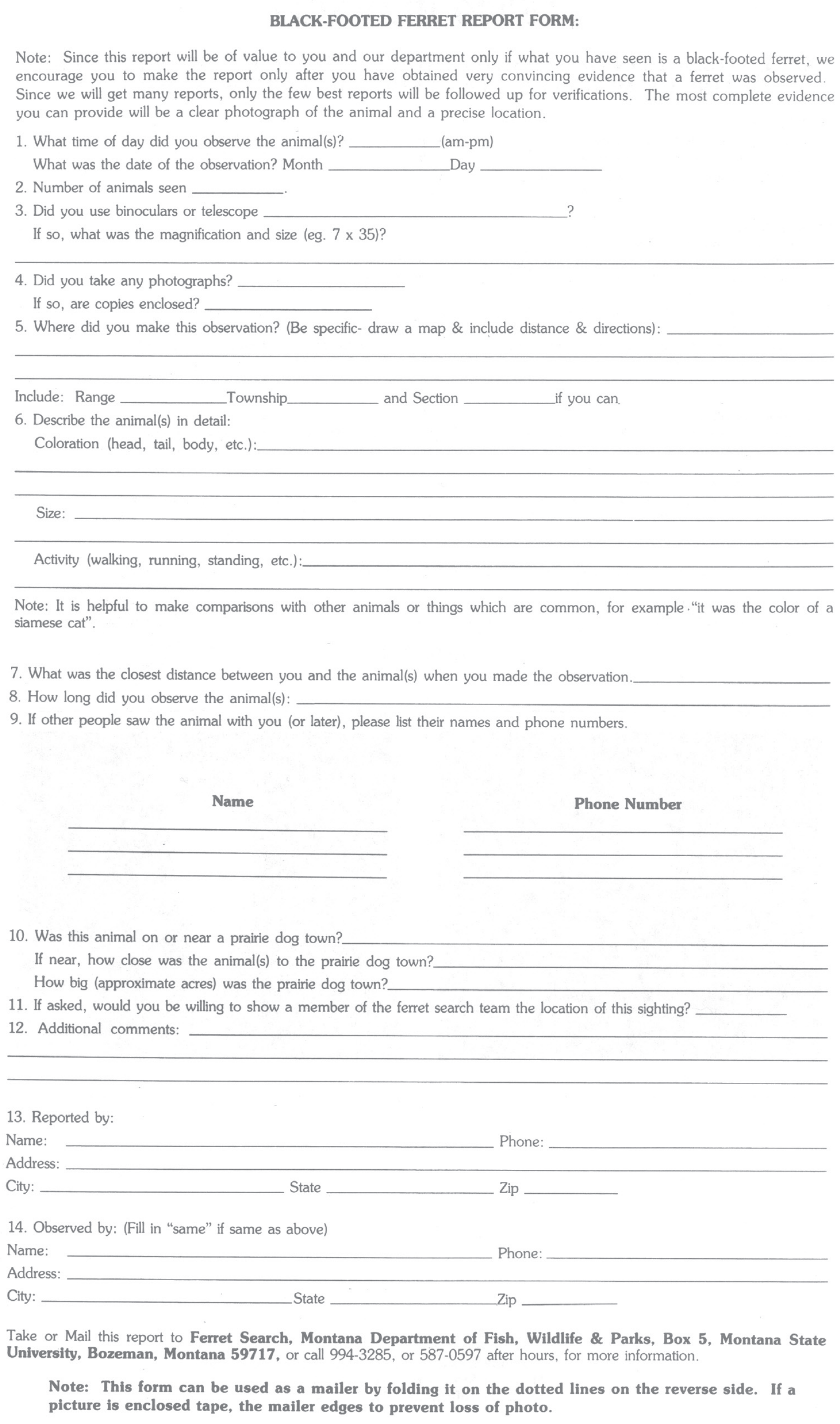
____

____

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: ____
    ____
    ____

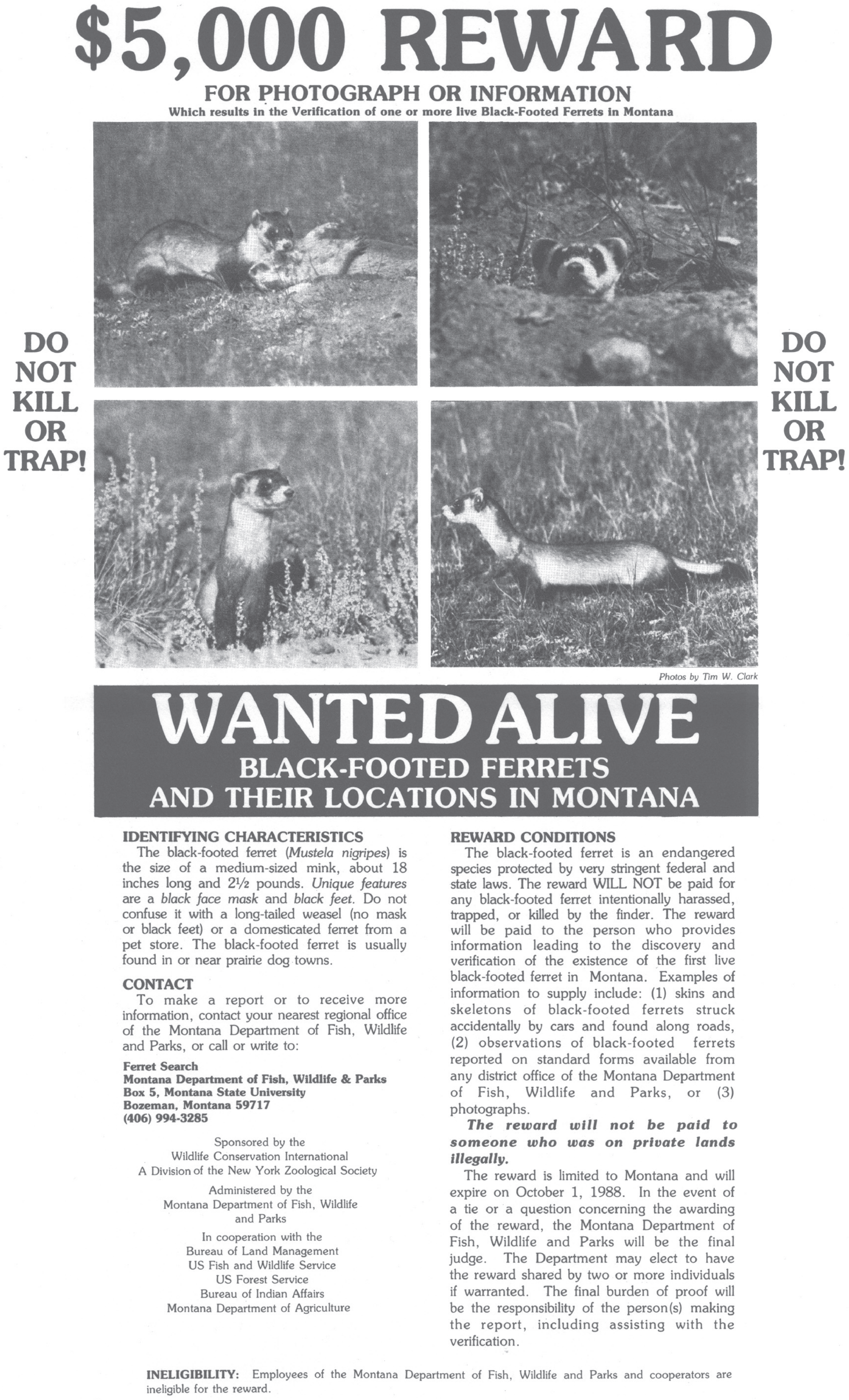
13. Reported by:
Name: ________________________________ Phone: ____________________
Address: ____
City: ____________________ State ______________ Zip __________

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

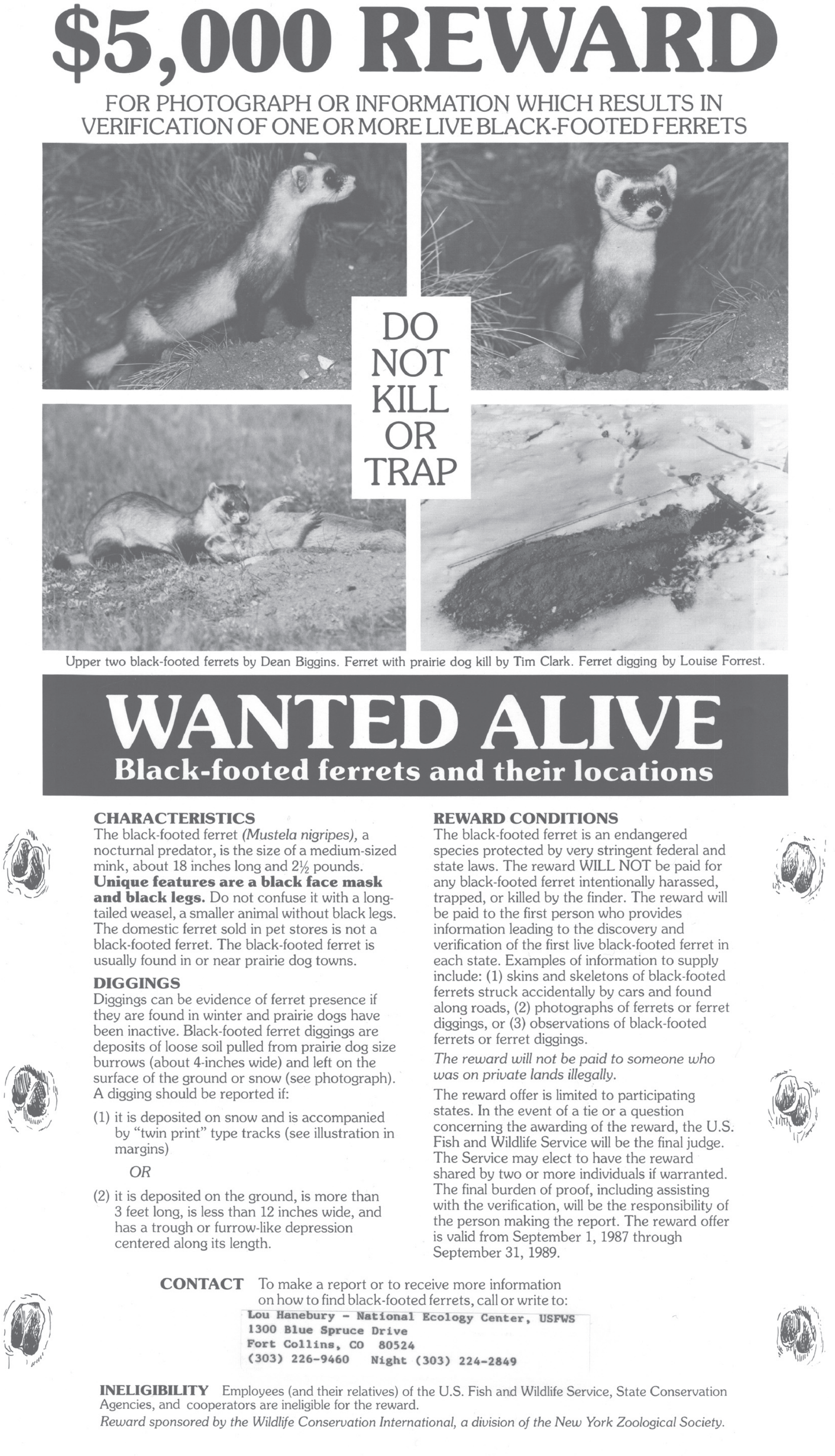
The black-footed ferret is an endangered species protected by very stringent federal and state laws. The reward WILL NOT be paid for any black-footed ferret intentionally harassed, trapped, or killed by the finder. The reward will be paid to the person who provides information leading to the discovery 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.

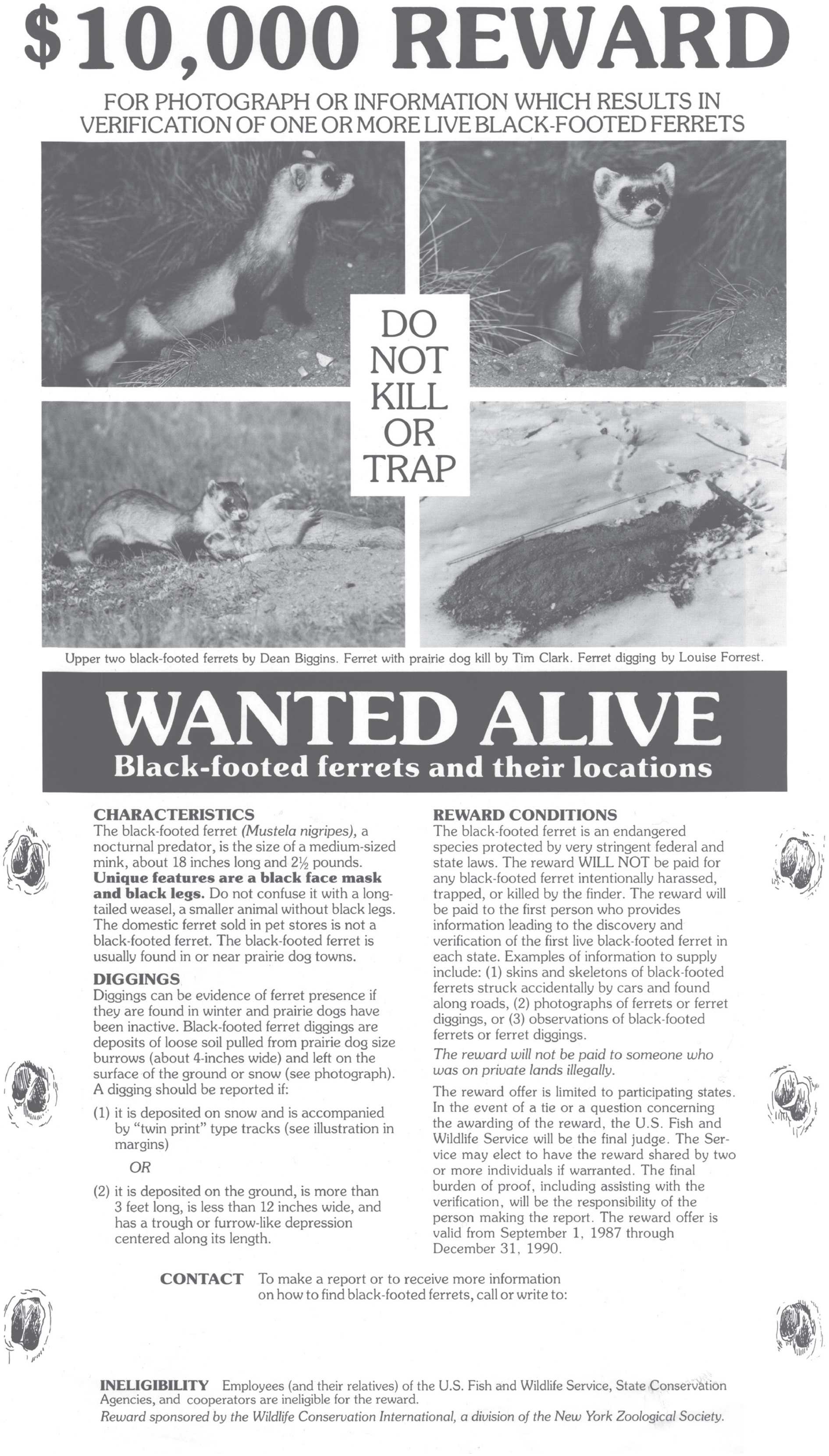
CONTACT To make a report or to receive more information on how to find black-footed ferrets, call or write to:

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:

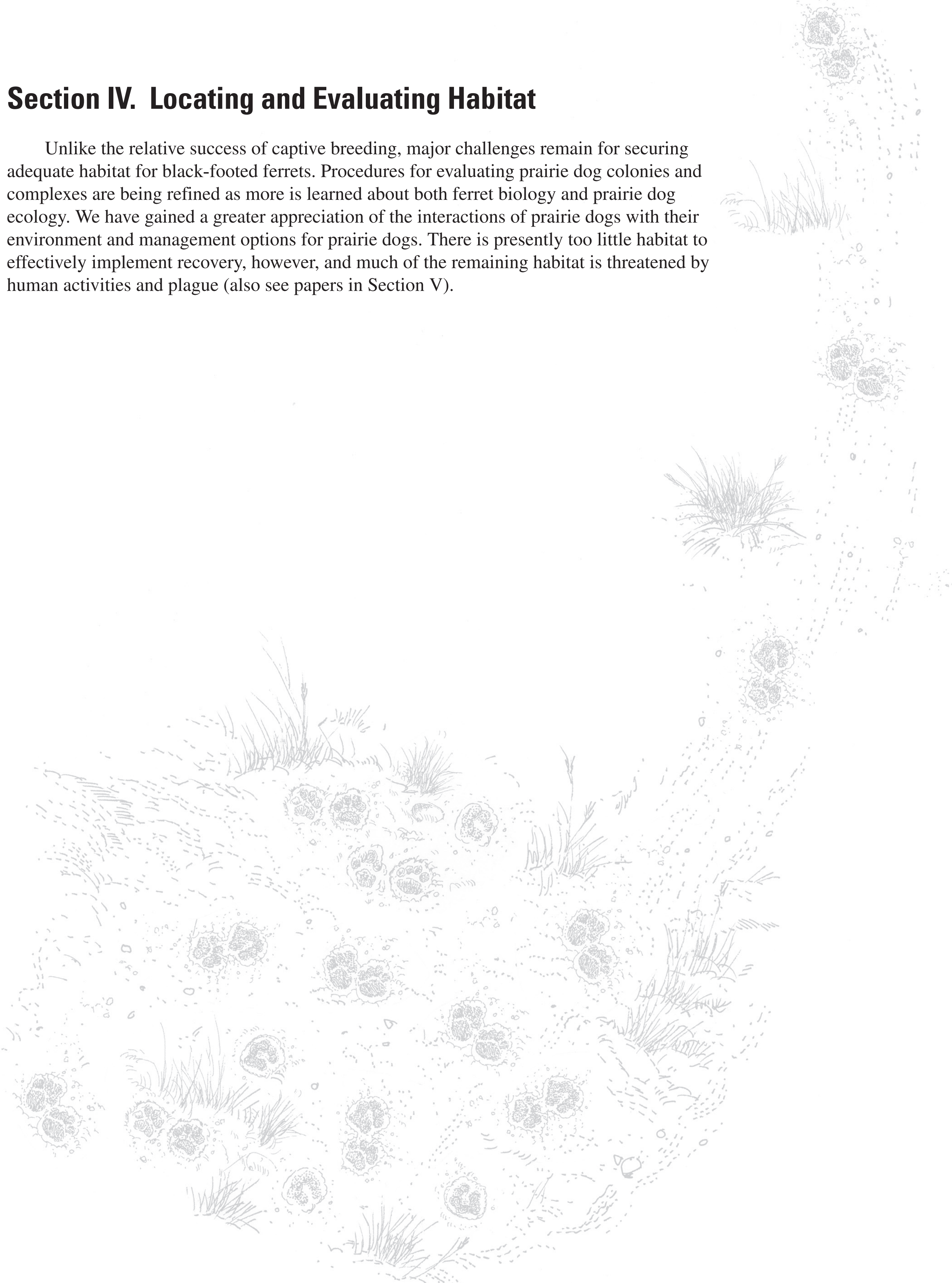
INELIGIBILITY Employees (and their relatives) of the U.S. Fish and Wildlife Service, State Conservation Agencies, and cooperators are ineligible for the reward.

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

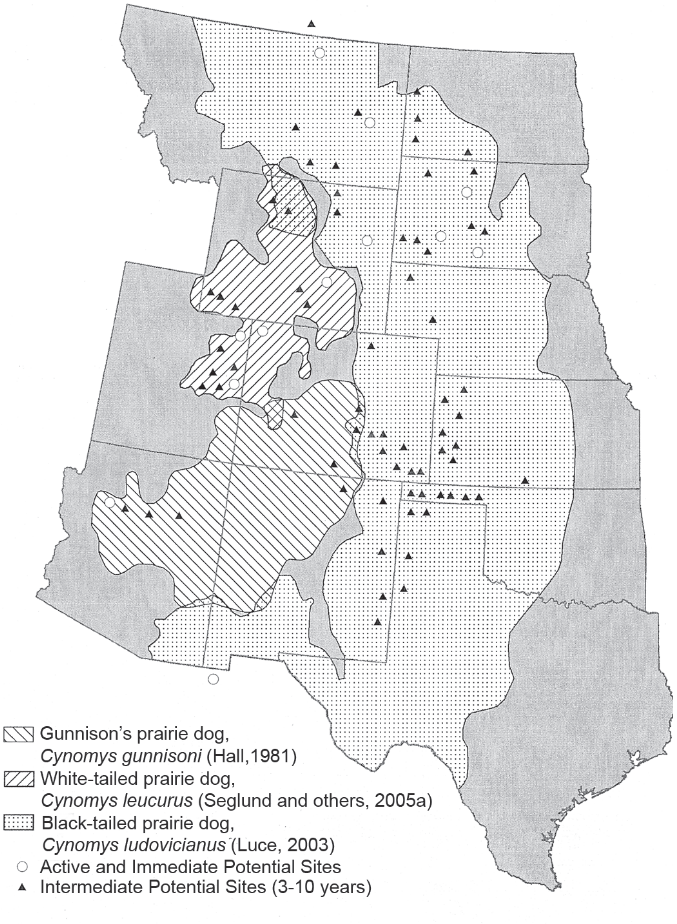


Figure 1. Location of eight active black-footed ferret (*Mustela nigripes*) reintroduction sites (1990–2004); three Immediate Potential Sites (1–3 years); and 70 Intermediate Potential Sites, at which, pending further evaluation, opportunities for reintroducing ferrets may exist in 3–10 years.

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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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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Crawford 92.

Habitat Restoration and Management

By Joe C. Truett,[1] Kristy Bly-Honness,[2] Dustin H. Long,[3] and Michael K. Phillips[4]

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

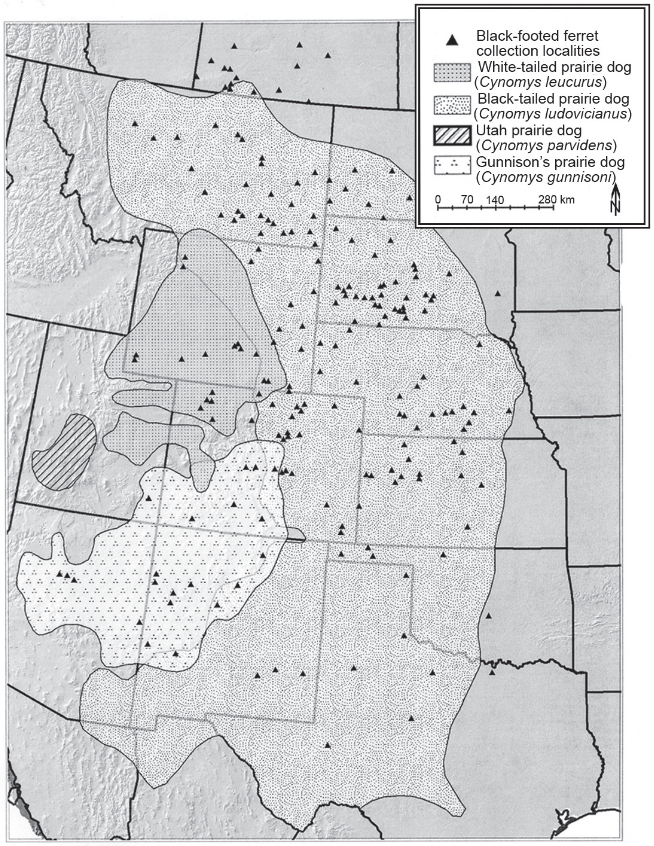

Figure 1. Collection locations for black-footed ferrets (*Mustela nigripes*) (Anderson and others, 1986) and historical ranges of prairie dogs (*Cynomys* spp.) across the Great Plains. Each collection location (dark triangle) represents ≥1 verified historical record(s).

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.

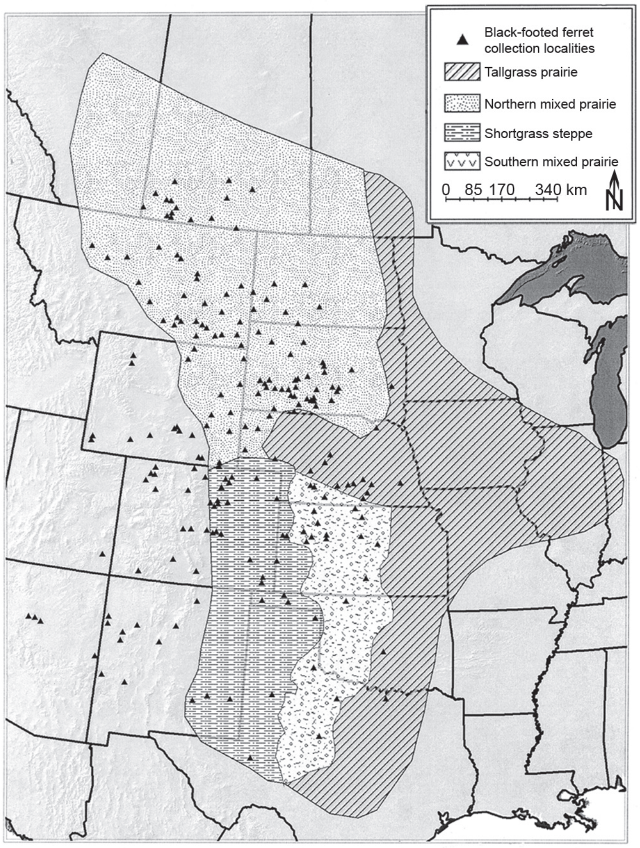

Figure 2. Collection locations for black-footed ferrets (*Mustela nigripes*) (Anderson and others, 1986) and distribution of Great Plains grassland types (Lauenroth and others, 1999). Each collection location (dark triangle) represents ≥1 verified historical record(s).

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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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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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 (≥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.

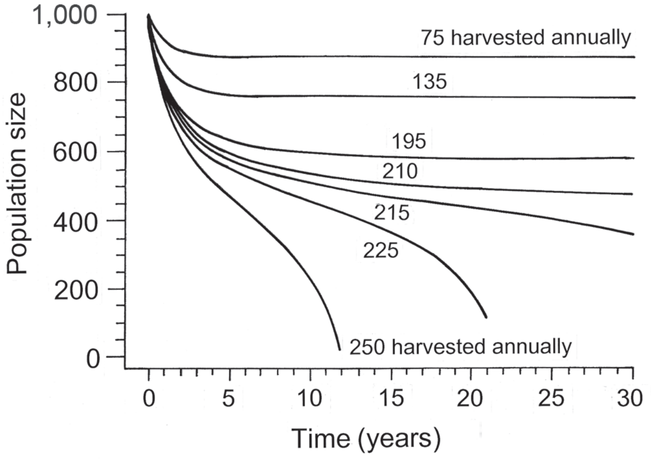

Figure 1. Effects of constant annual harvest quotas on a population with density-dependent growth (R_{max} = 2.00, K = 1,000) but no random variation in R_t. Annual harvest >209 animals (maximum yield) cannot be sustained, and the population eventually declines to zero.

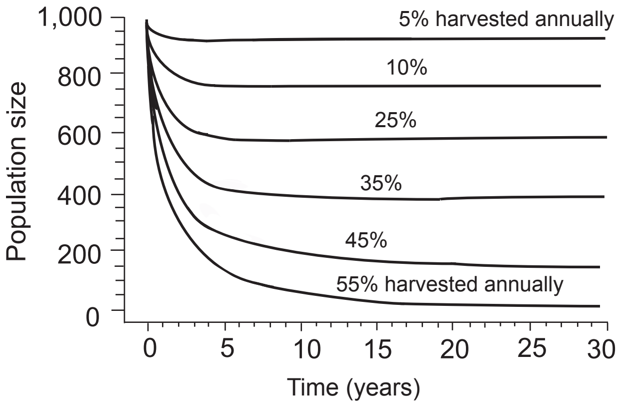

Figure 2. Deterministic predictions of a population with density-dependent growth (R_{max} = 2.00, K = 1,000) subject to different levels of proportional harvest annually.

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).

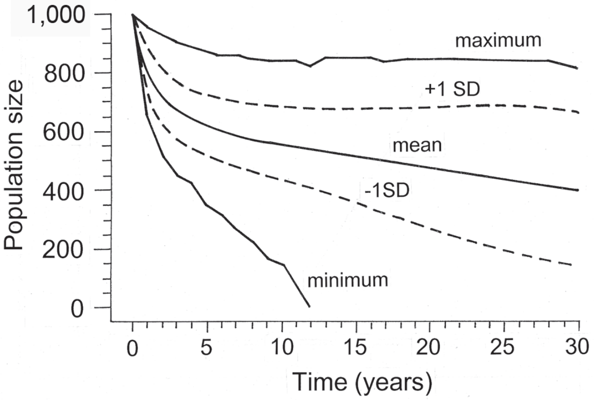

Figure 4. Results of 1,000 simulations with an annual harvest quota of 195 animals, an initial population of 1,000 animals, density-dependent population growth ($R_{max} = 2.00$), and random variation in the population growth rate each year (within ±15% of R_t after computation as $R_t = R_{max}^{(1 - Nt/K)}$).

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

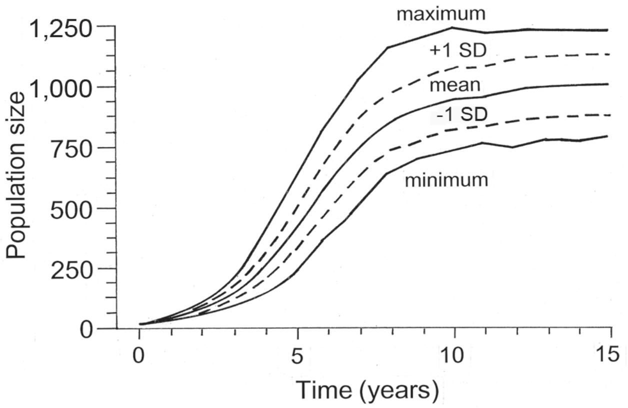

Figure 3. Results of 100 simulations of density-dependent population growth ($R_{max} = 2.00$, $K = 1{,}000$), but with random variation in the population growth rate each year (within ± 20% of R_t after computation as $R_t = R_{max}^{(1 - Nt/K)}$).

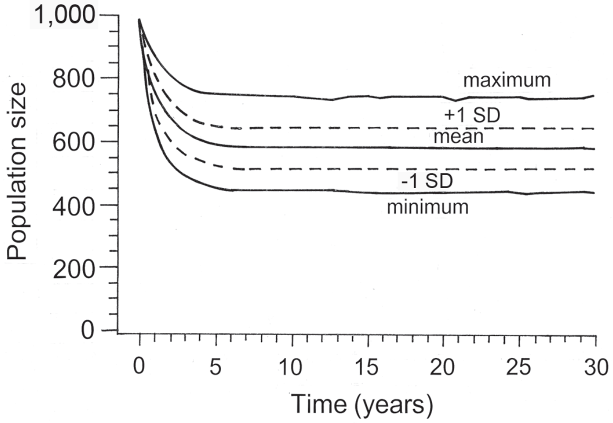

Figure 5. Results of 1,000 simulations with an annual harvest rate of 25%, an initial population of 1,000 animals, density-dependent population growth with $R_{max} = 2.00$, and random variation in the population growth rate each year (within ±15% of R_t after computation as $R_t = R_{max}^{(1 - Nt/K)}$).

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.

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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

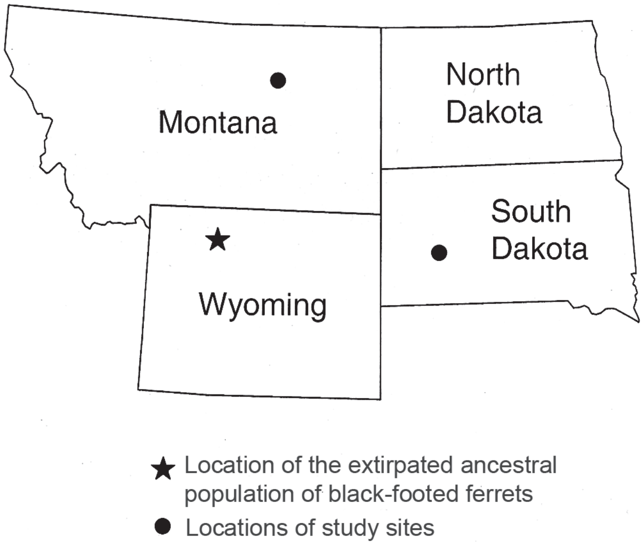

Figure 1. The site near Meeteetse, Wyo., that provided ancestral stock for the captive breeding program, and study sites in Montana and South Dakota where black-footed ferrets (*Mustela nigripes*) were released.

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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

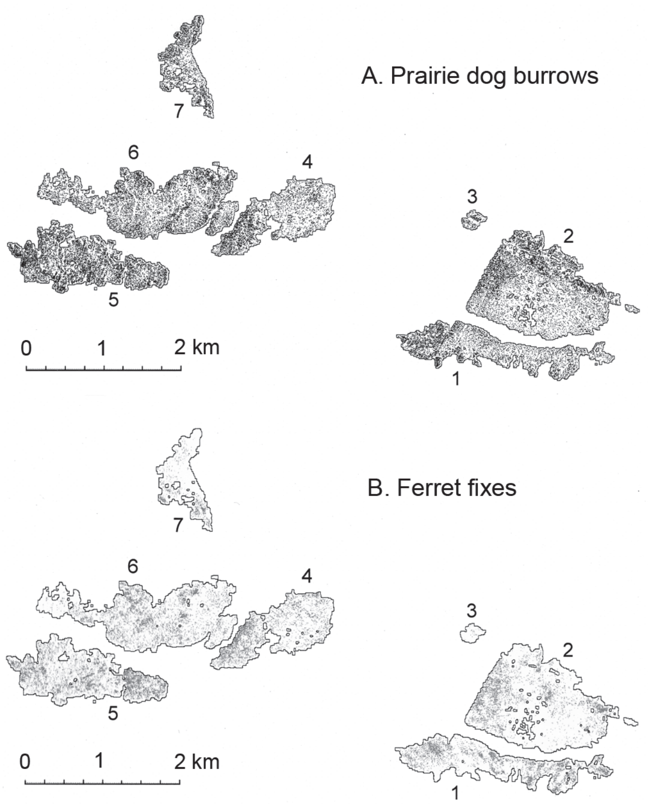

Figure 2. Distribution of black-tailed prairie dog (*Cynomys ludovicianus*) burrows (A) and black-footed ferret (*Mustela nigripes*) telemetric fixes (B) on colonies at UL Bend National Wildlife Refuge, Mont. Each dot is a burrow opening or telemetric fix; density of resulting stippling thus reflects 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.

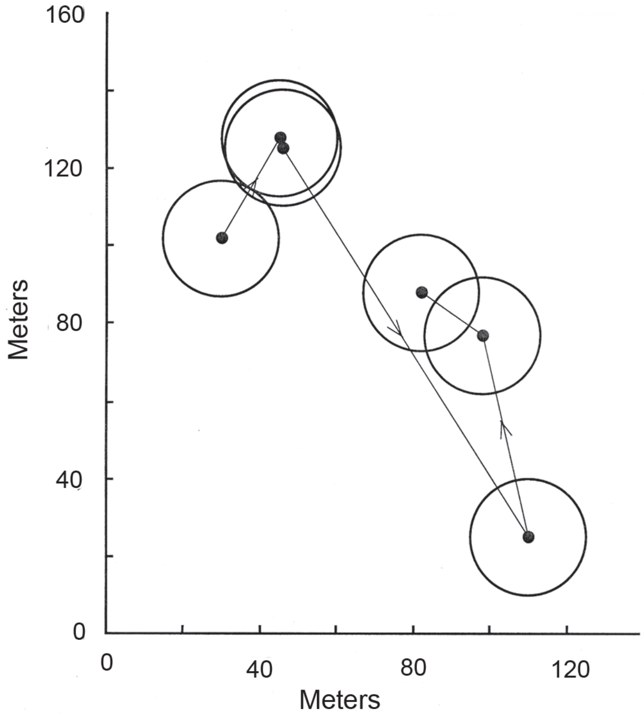

Figure 3. Example of encircling a series of telemetric fixes with plots of 15-m radius, within which black-tailed prairie dog (*Cynomys ludovicianus*) burrow entrances were counted, for black-footed ferret (*Mustela nigripes*) no. 32, North Sage Creek, S. Dak., on the night of October 26–27, 1997. Overlapping 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

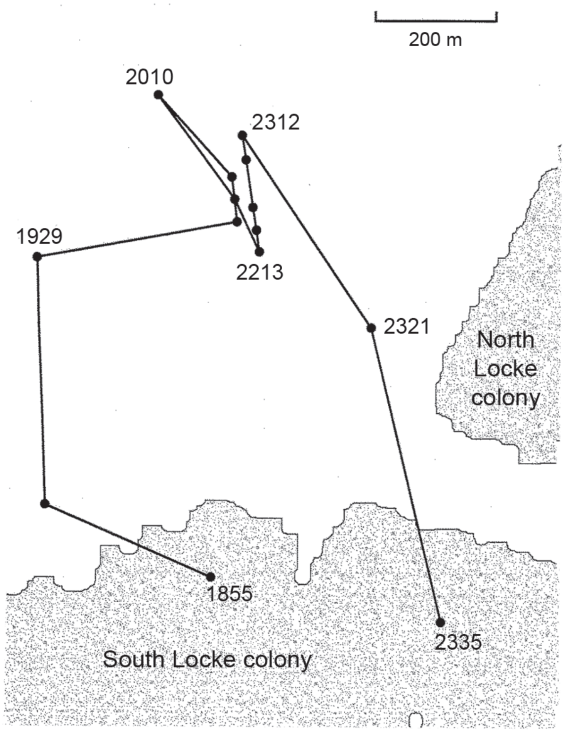

Figure 4. An example of an exploratory excursion away from a black-tailed prairie dog (*Cynomys ludovicianus*) colony by young male black-footed ferret (*Mustela nigripes*) no. 24, UL Bend National Wildlife Refuge, Mont., October 20, 1994. Numbers associated with points are times of day.

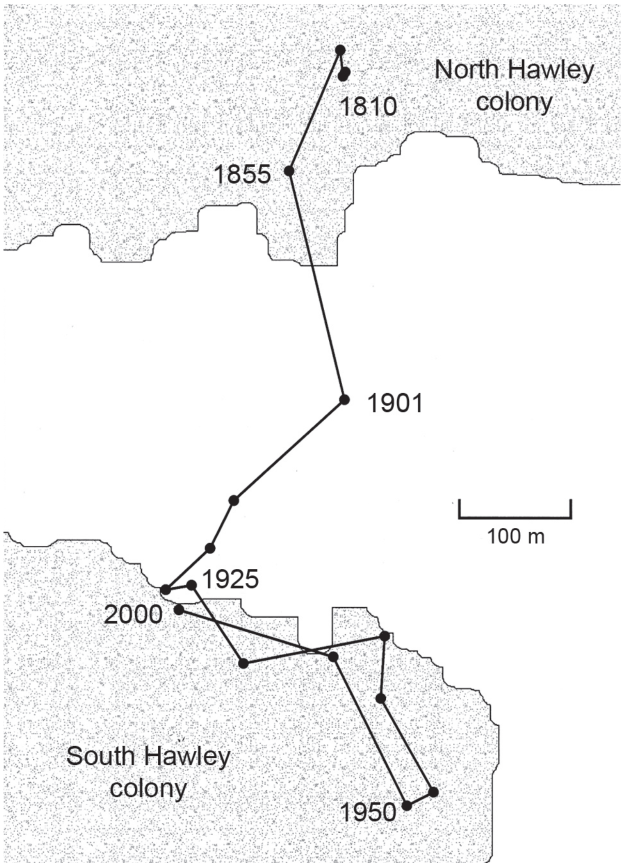

Figure 5. An example of an intercolony move by young female black-footed ferret (*Mustela nigripes*) no. 71, UL Bend National Wildlife Refuge, Mont., November 5, 1995. Numbers associated with points are times of day.

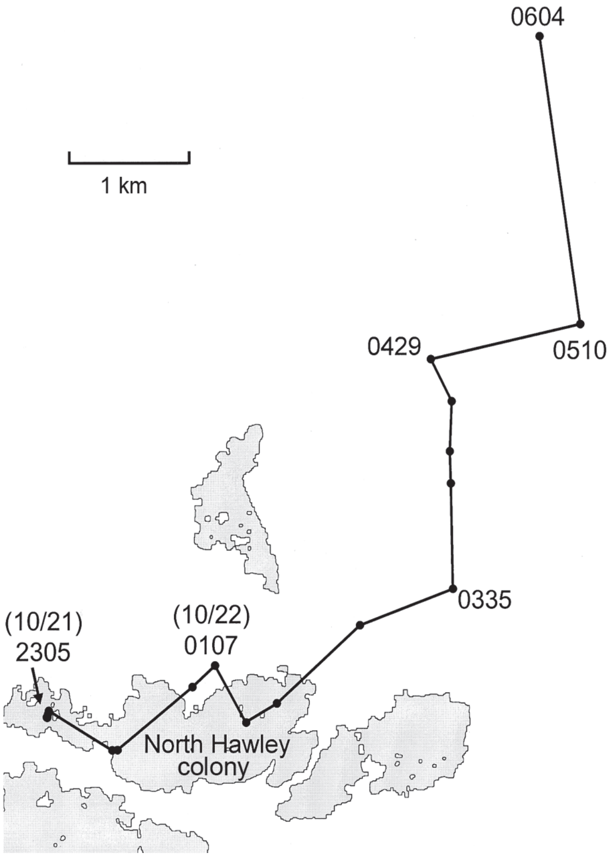

Figure 6. An example of dispersal away from black-tailed prairie dog (*Cynomys ludovicianus*) colonies by young male black-footed ferret (*Mustela nigripes*) no. 213, October 21–22, 1997. Numbers associated with points are times of day.

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

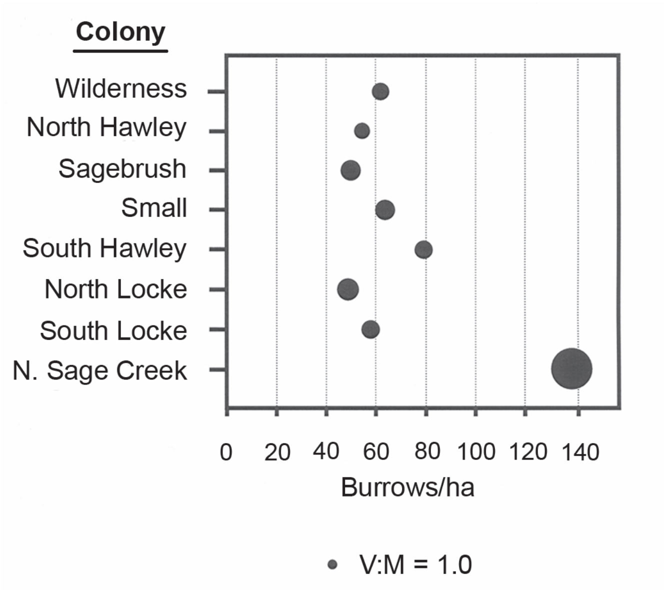

Figure 7. Densities of burrows on study colonies and variance to mean ratios (V:M) estimated from samples of 0.07-ha plots. Diameter of symbol is proportionate to V:M ratio within sample of plots.

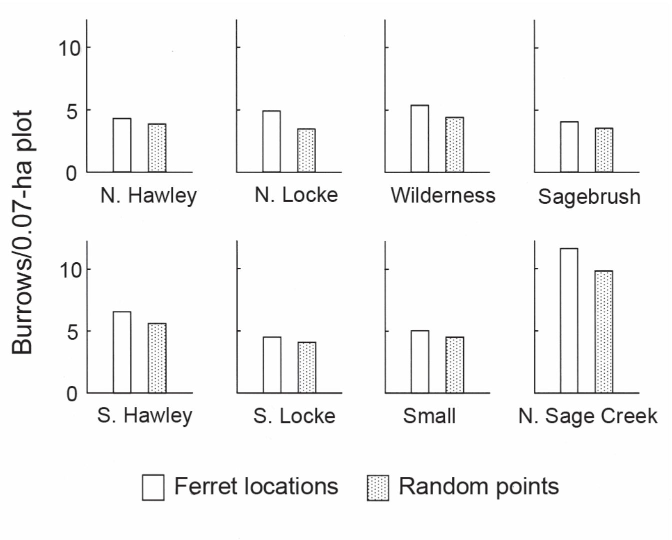

Figure 8. Burrow densities within plots encircling telemetric fixes of black-footed ferrets (*Mustela nigripes*) and within plots at random points on black-tailed prairie dog (*Cynomys ludovicianus*) colonies.

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.

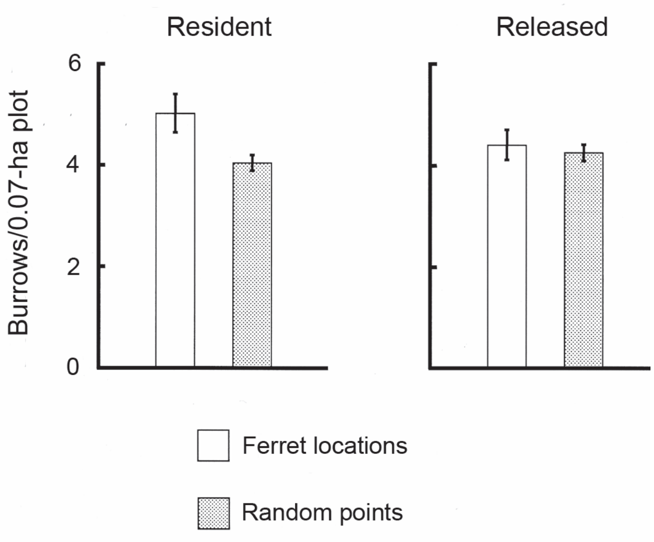

Figure 9. Densities of burrows (mean ± SE) in areas used by (and available to) black-footed ferret (*Mustela nigripes*) kits released into ferret-occupied habitat at Hawley Flats Mont., in 1997, and densities of burrows in habitat used by (and available to) the resident wild-born ferret kits at that site.

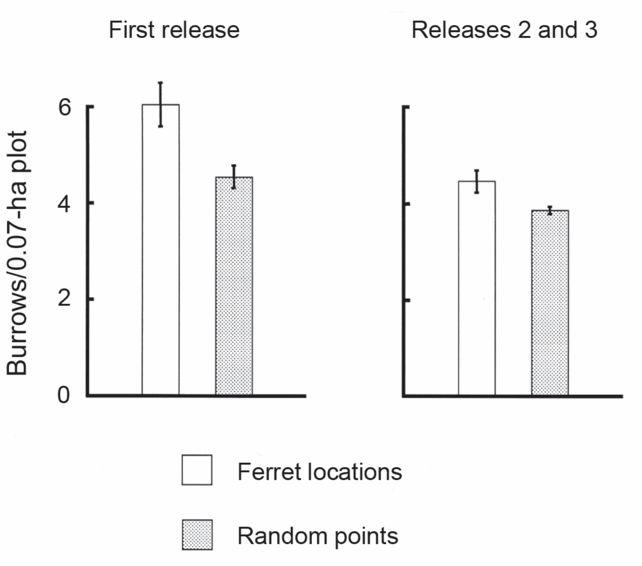

Figure 10. Densities of burrows (mean ± SE) in areas used by (and available to) the first black-footed ferret (*Mustela nigripes*) kits released at Locke Ranch and Hawley Flat, Mont., in 1994 and 1995, and densities of burrows in areas used by (and available to) ferret kits after subsequent releases during those years at those sites.

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.

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

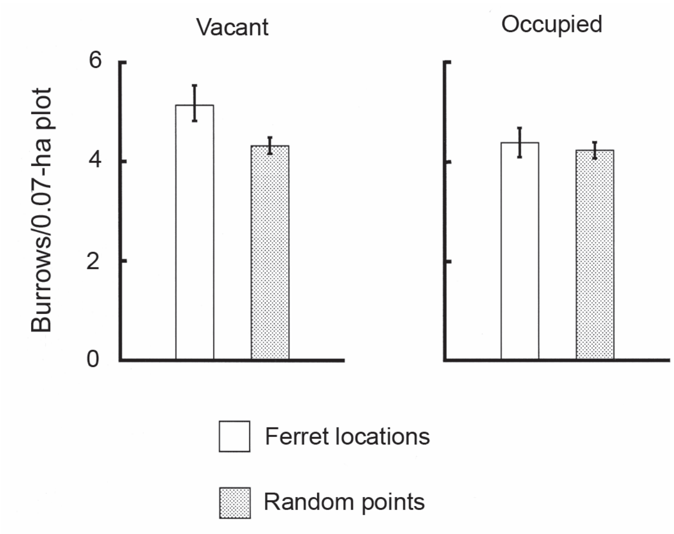

Figure 11. Densities of burrows (mean ± SE) in areas used by (and available to) black-footed ferret (*Mustela nigripes*) kits released into ferret-unoccupied habitat at Hawley Flat, Mont., in 1995, and densities of burrows in areas used by (and available to) ferret kits released to augment the extant 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.

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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).

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).

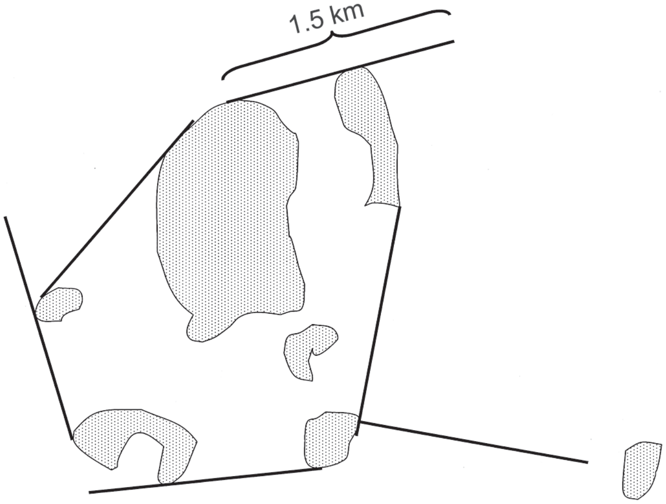

Figure 1. Procedure for circumscribing a subcomplex of prairie dog (*Cynomys* spp.) colonies by using a minimum intercolony distance of 1.5 km. See Biggins and others (1993) for additional details on the methodology.

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.

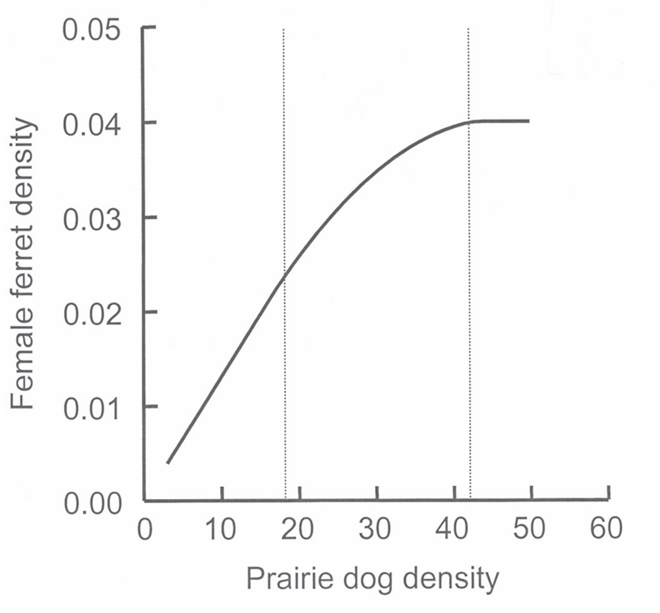

Figure 2. Hypothetical relationship between densities of prairie dogs (*Cynomys* spp.) and densities of female black-footed ferrets (*Mustela nigripes*) (individuals/ha), allowing territoriality to modify the linear relationship predicted by the energetics-based equation ($Y = X/763$) of Biggins and 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

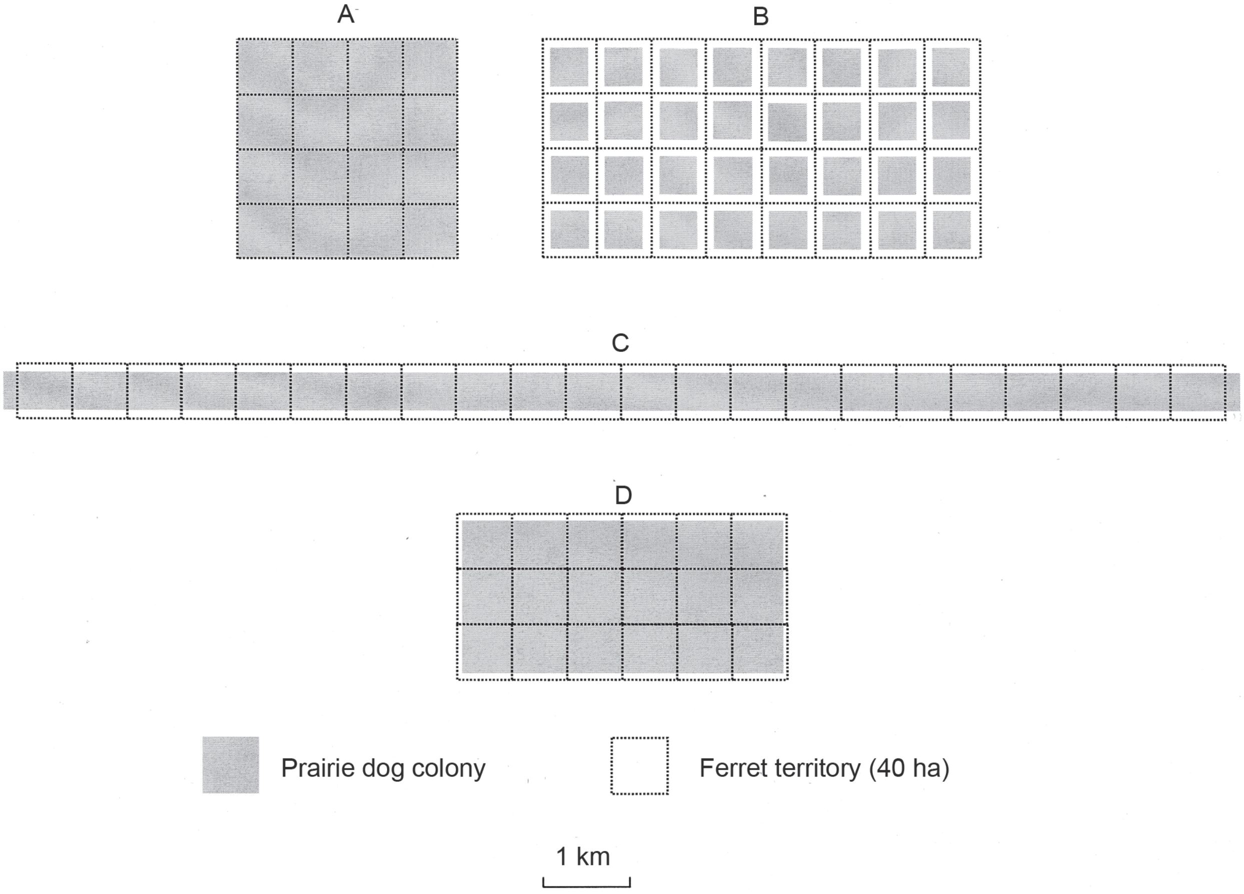

Figure 3. Comparison of female black-footed ferret (*Mustela nigripes*) numbers supported by hypothetical prairie dog (*Cynomys* spp.) complexes occupying 640 ha: (A) a complex with a single square colony (*n* = 16 ferrets); (B) a complex with 20-ha colonies at sufficient spacing to allow separate ferret 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.

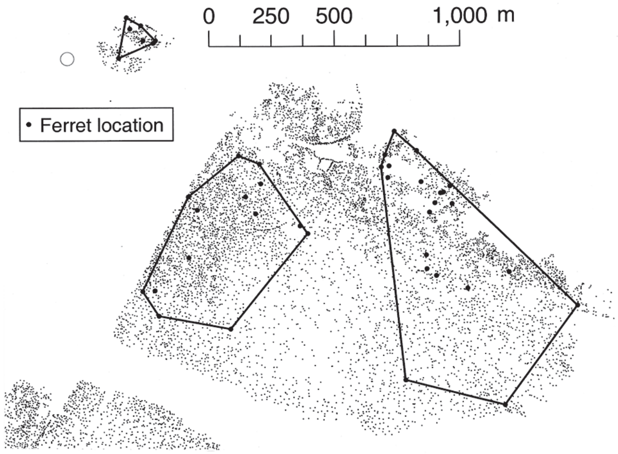

Figure 4. Activity areas (circumscribed by minimum convex polygons) for three female black-footed ferrets (*Mustela nigripes*) with litters. These females and their litters were repeatedly relocated during summer 1998 at UL Bend National Wildlife Refuge, Mont. Heterogeneity in dispersion of black-tailed 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

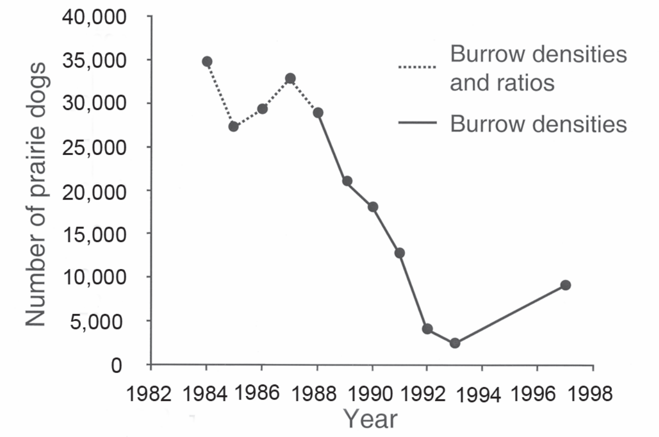

Figure 5. Estimates of white-tailed prairie dogs (*Cynomys leucurus*) on the Meeteetse, Wyo., complex, derived from estimates of active burrow density (Biggins and others, 1993). (Adapted from Biggins and Kosoy, 2001. Reprinted with permission of the *Journal of the Idaho Academy of Science*, Pocatello, 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.

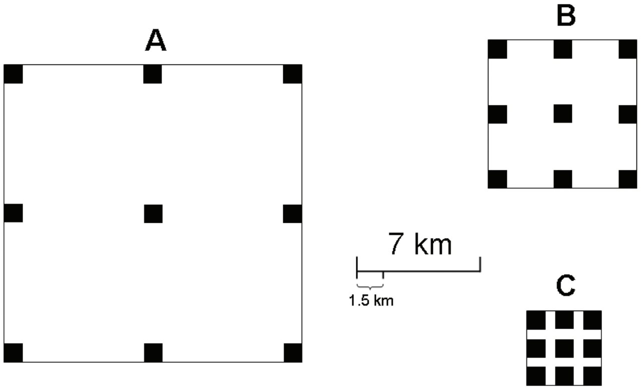

Figure 6. In these three hypothetical complexes, total area occupied by prairie dog (*Cynomys* spp.) colonies (shaded squares) is the same (1,000 ha), but the percentages of each complex occupied by colonies are 4%, 14%, and 57% for A, B, and C, respectively. Are the complexes of equal quality as habitat 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.

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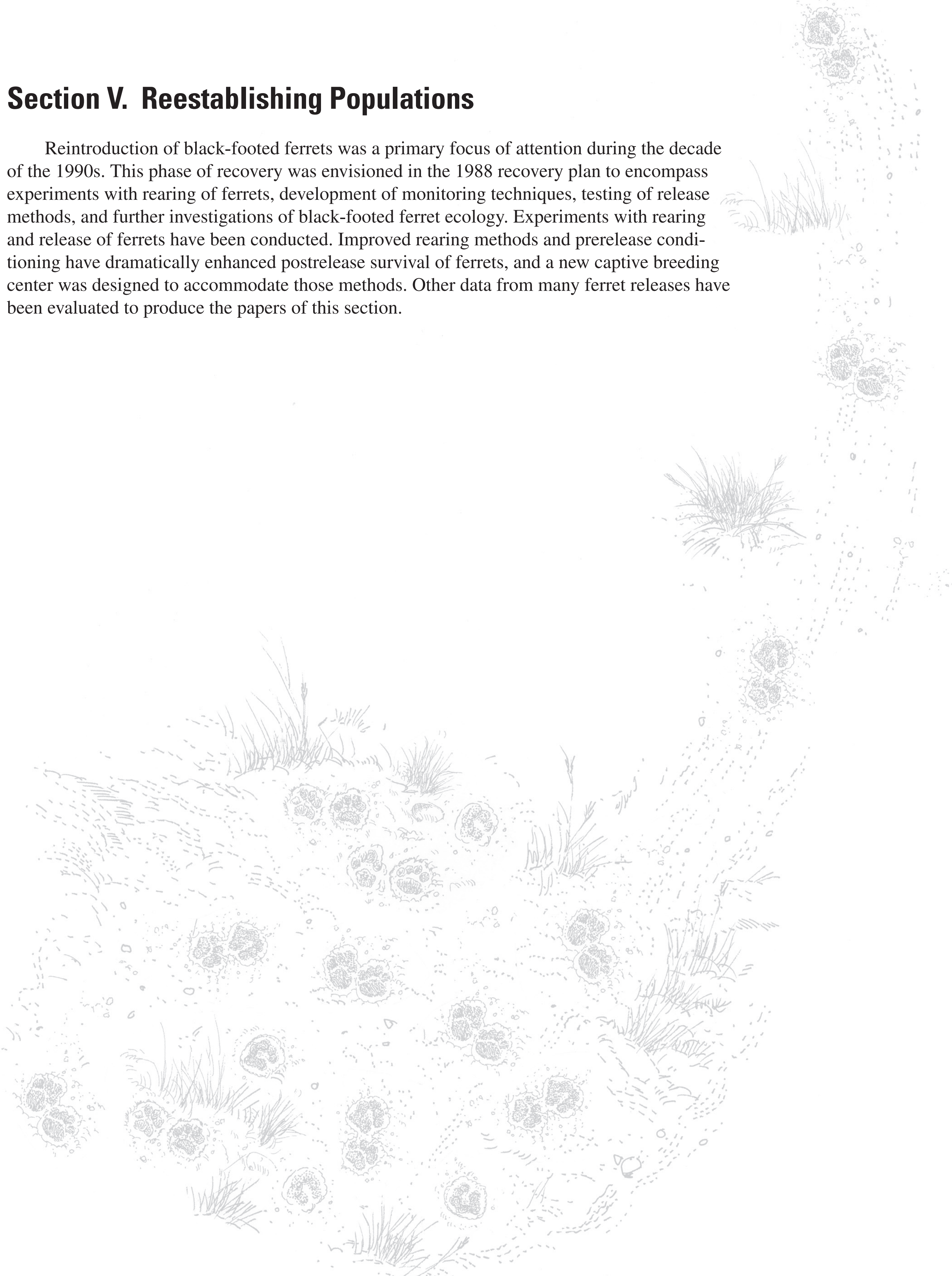
Section V. Reestablishing Populations

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).

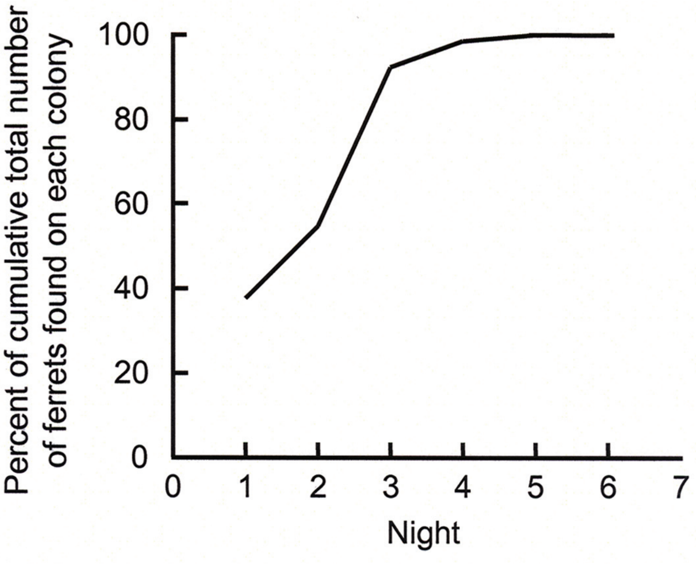

Figure 1. Black-footed ferrets (*Mustela nigripes*) encountered per night during spotlight searches on 17 black-tailed prairie dog (*Cynomys ludovicianus*) colonies, September 16-22, 2002, in Conata Basin, S. Dak.

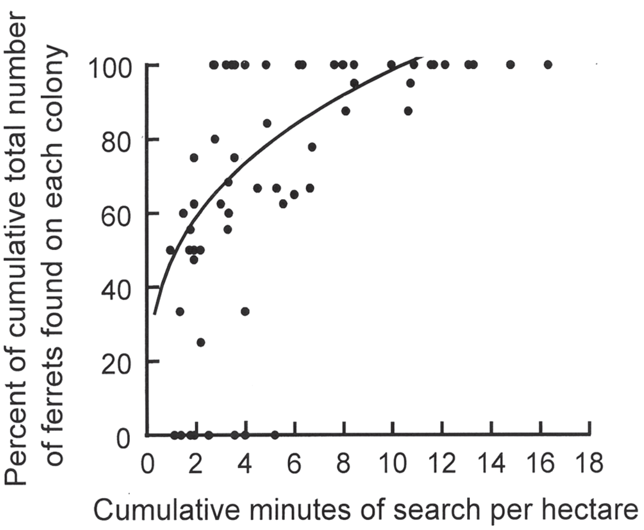

Figure 2. Black-footed ferrets (*Mustela nigripes*) encountered per minute per hectare during spotlight searches on 17 black-tailed prairie dog (*Cynomys ludovicianus*) colonies, September 16-22, 2002, in Conata Basin, S. Dak. An exponential curve was fitted to data.

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

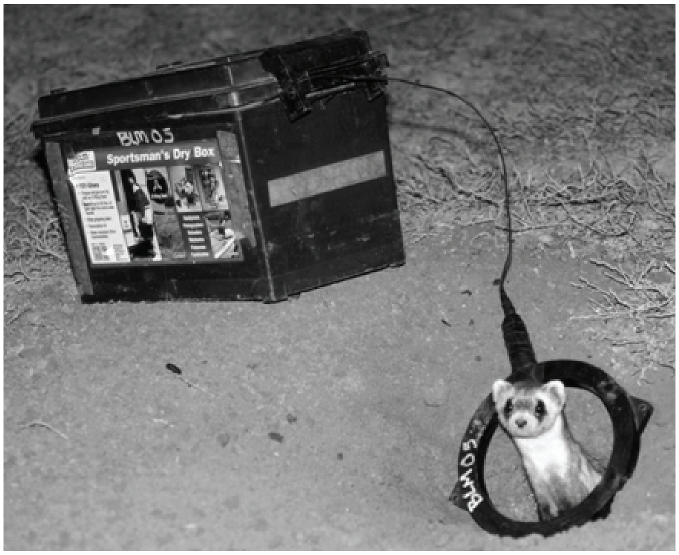

Figure 3. Automated passive integrated transponder readers in waterproof boxes may be left at burrows occupied by black-footed ferrets (*Mustela nigripes*). Transponder numbers will be recorded as the ferret passes near (or through) the loop antenna placed to encircle the burrow entrance.

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

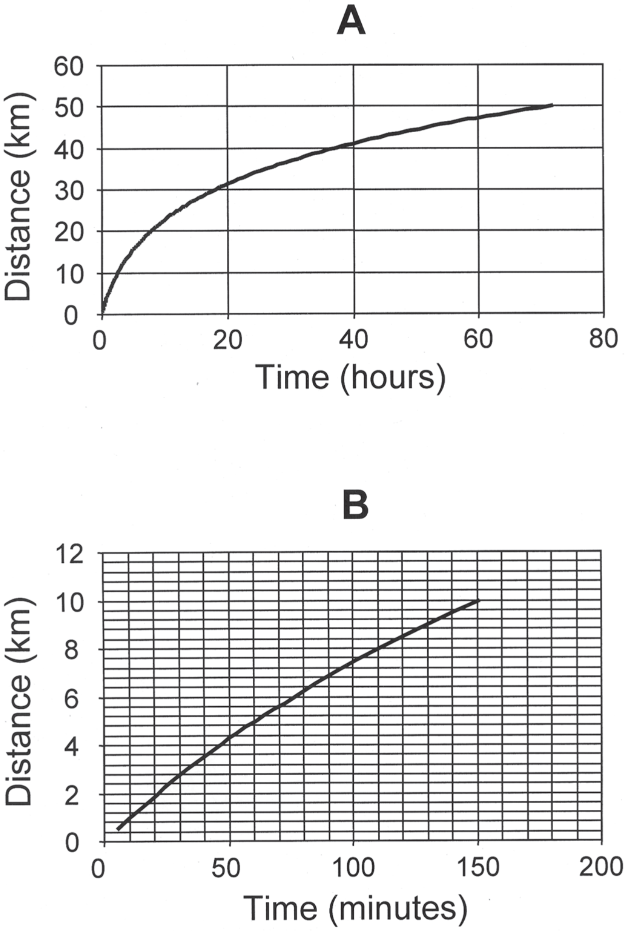

Figure 4. Minimum separations of distance and time needed to classify two sightings of black-footed ferrets (*Mustela nigripes*) as different individuals. Plot B is the lower portion of the curve in plot A, rescaled to provide better resolution. Separations of two sightings plotting above the curves 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).

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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

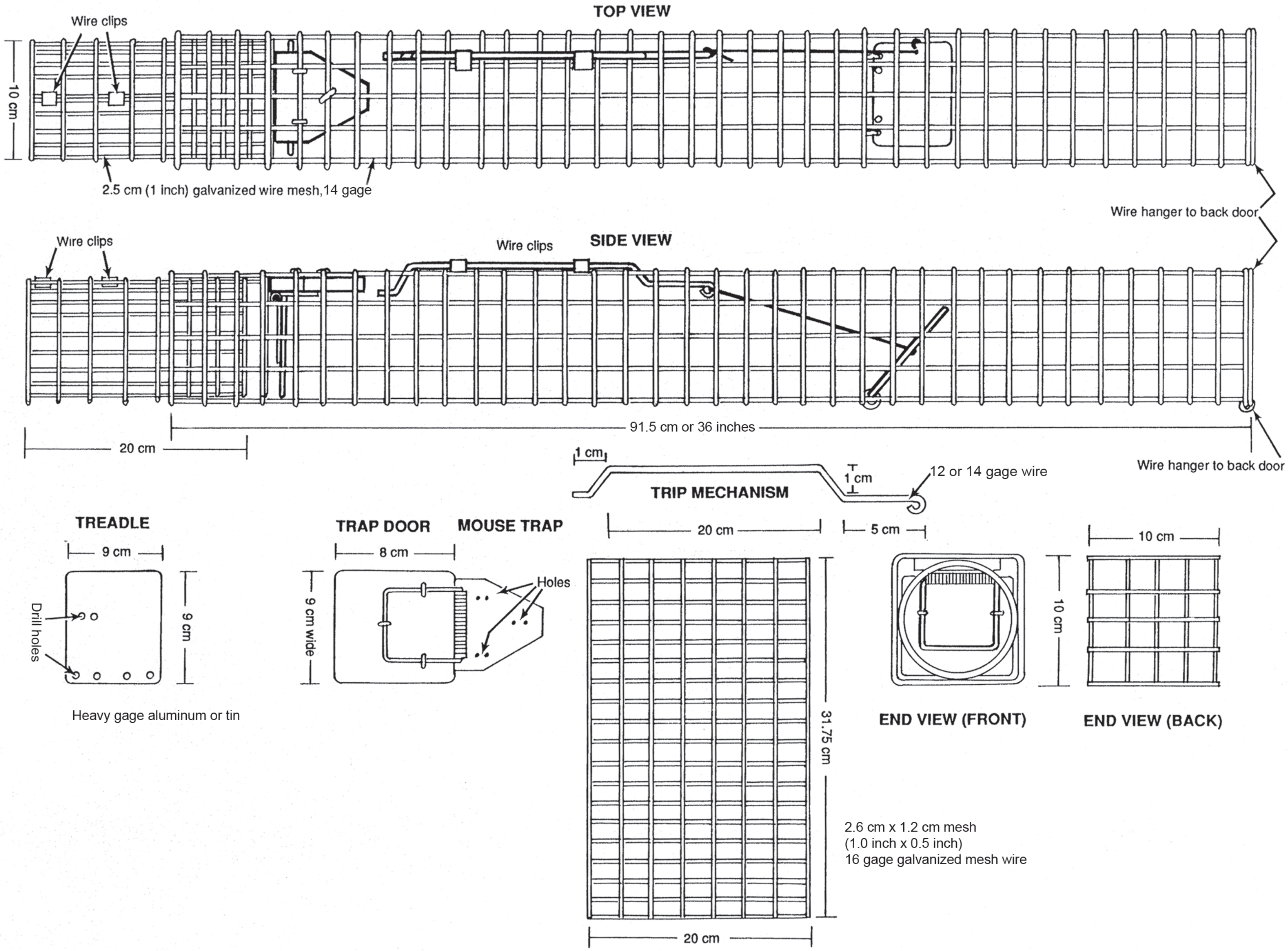

Figure A1. Design of a trap for black-footed ferrets (*Mustela nigripes*). This trap is a modification of the model described by Sheets (1972).

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.

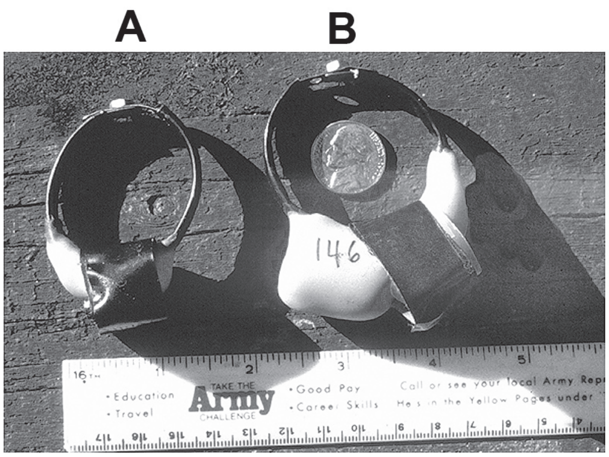

Figure 1. The first radio collars tested for use on black-footed ferrets (*Mustela nigripes*), ca. 1979 (version A-1 of table 1). A model similar to “A” was used on ferrets. Photograph by D. Biggins.

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 Width[2]	Pulse Rate[3]	Battery life (days)
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.

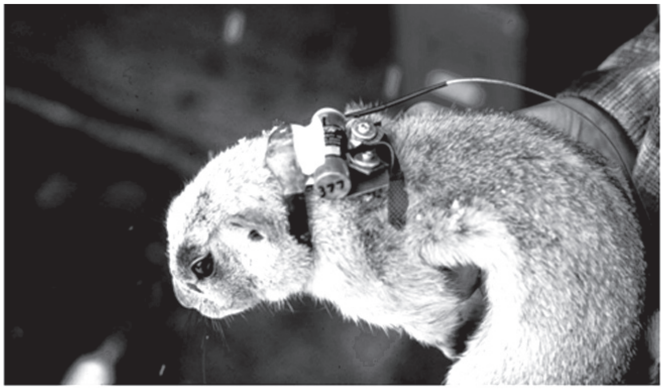

Figure 3. Capsules with high power output (Telonics, Inc., Mesa, Ariz.) (version B-1 of table 1) were attached to harnesses and tested on surrogate prairie dogs (*Cynomys* spp.) in 1982. Photograph by D. Biggins.

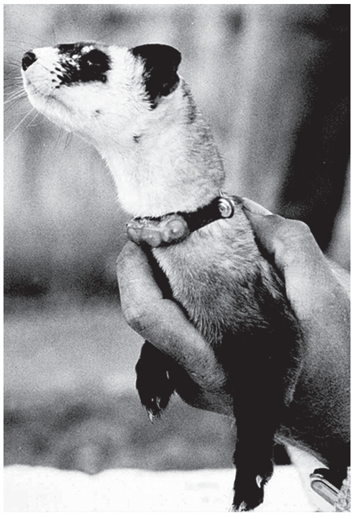

Figure 4. A 13-g transmitter package (version D-1 of table 1) used on black-footed ferrets (*Mustela nigripes*) during 1983–84. Photograph by D. Biggins.

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.

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

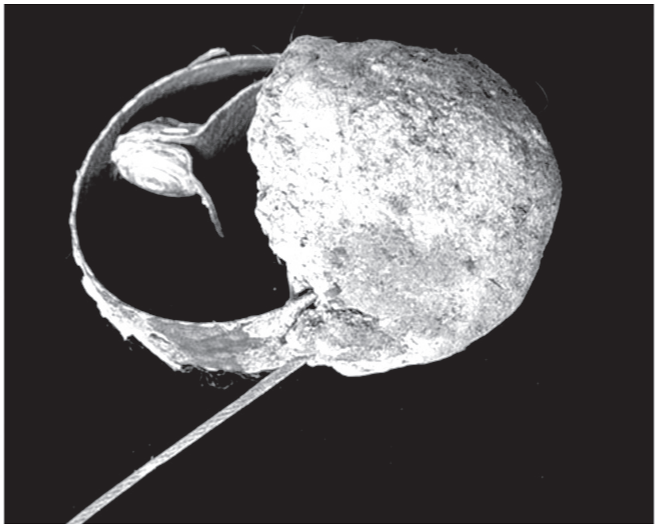

Figure 6. A collar from 1983 that accumulated a large buildup of clay while carried by a black-footed ferret (*Mustela nigripes*). Photograph by D. Biggins.

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

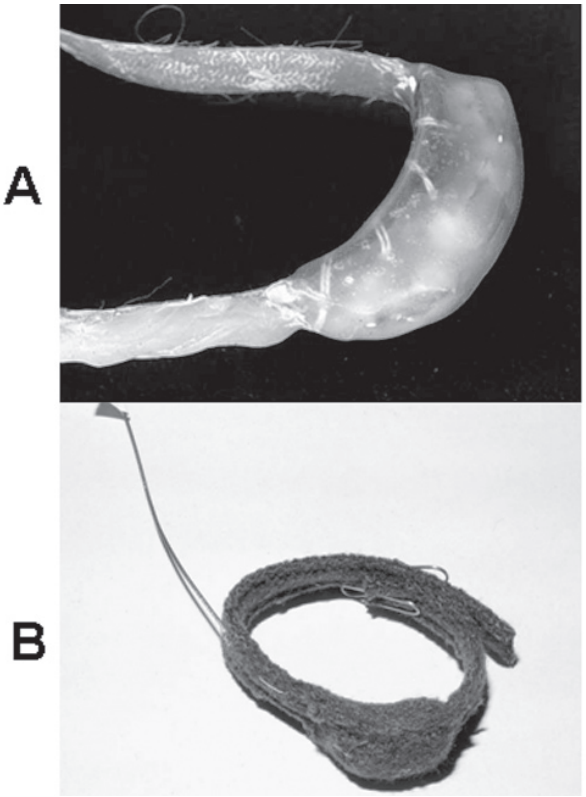

Figure 7. The acrylic potting material was polished (A) or encased in wool (B) in attempts to alleviate mud accumulation. Photograph by D. Biggins.

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.

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.

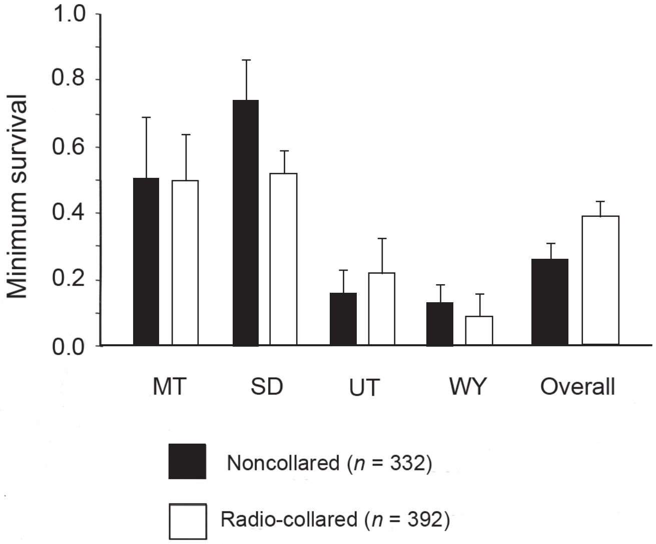

Figure 12. Minimum survival rates of preconditioned black-footed ferret (*Mustela nigripes*) kits at about 1 month postrelease.

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).

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 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.

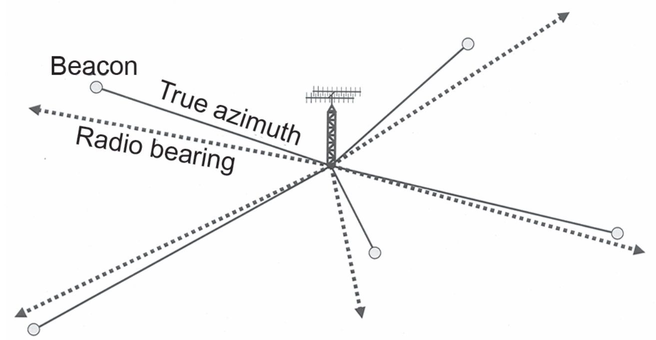

Figure 15. Accuracy testing and referencing involve comparison of true azimuths and radio bearings to beacon transmitters.

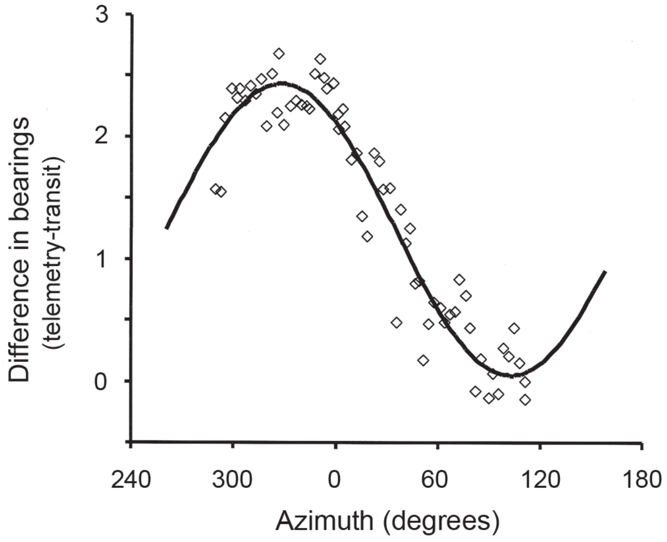

Figure 16. An accuracy test done at station 4, UL Bend National Wildlife Refuge, Mont., 1994. In this case, bias was corrected by using a formula defining the sine curve plotted. Residual variation produced a bias-adjusted accuracy estimate of ±0.63° (90% confidence) for future bearings from this station.

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

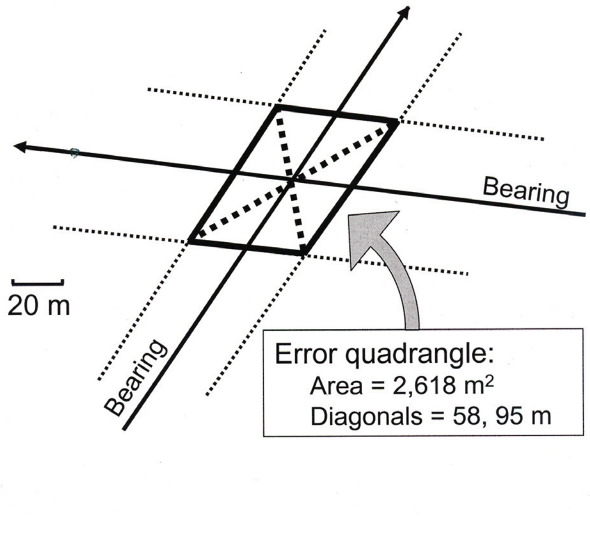

Figure 17. An example of a telemetric fix and error quadrangle (black-footed ferret [*Mustela nigripes*] no. 26, South Dakota, 10/23/97, 0148 h) produced by intersecting bearings and their associated error arcs from two tracking stations.

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

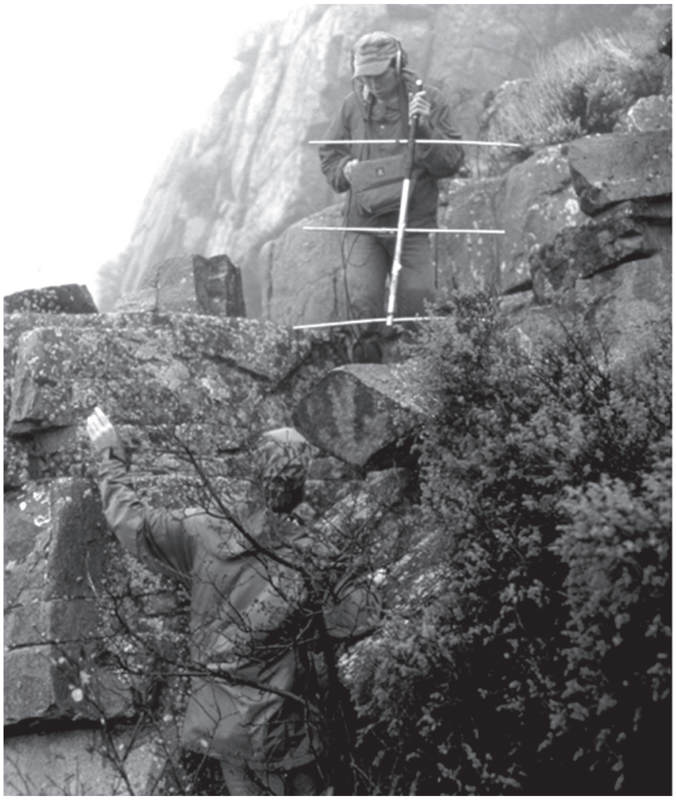

Figure 18. Hand tracking enabled us to locate black-footed ferrets (*Mustela nigripes*) that had dispersed into unusual habitats. Photograph by M. Albee.

Figure 19. Siberian polecat (*Mustela eversmannii*) killed by a predator. Photograph by D. Biggins.

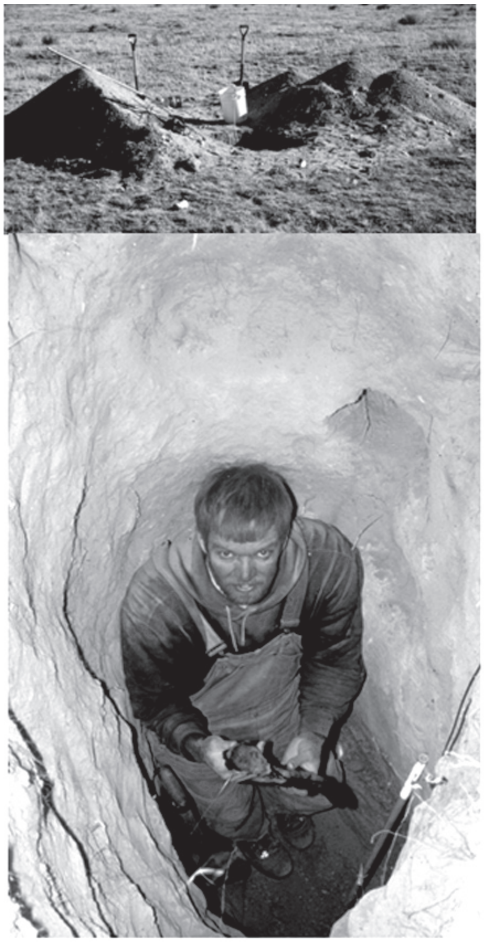

Figure 20. Hand-held tracking equipment enabled location of transmitters below ground, necessitating excavation to determine fate of animals such as this Siberian polecat (*Mustela eversmannii*) killed by a badger (*Taxidea taxus*). Photographs by D. Biggins.

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.

Acknowledgments

We thank the electronics laboratory of L. Kolz, of the former Denver Wildlife Research Center (U.S. Fish and Wildlife Service), for testing power output and other attributes of prototype implant and collar-mounted transmitters. Evaluations of prototype transmitters would not have been possible without sincere efforts and special attention of engineers and technicians at Advanced Telemetry Systems (Isanti, Minn.), AVM Instrument Company, Ltd., Custom Telemetry and Consulting (Watkinsville, Ga.), Telonics, Inc., and Wildlife Materials, Inc. We appreciate the dedication of the many technicians over a 20-year period that assisted with setting up, testing, and operating tracking stations.

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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

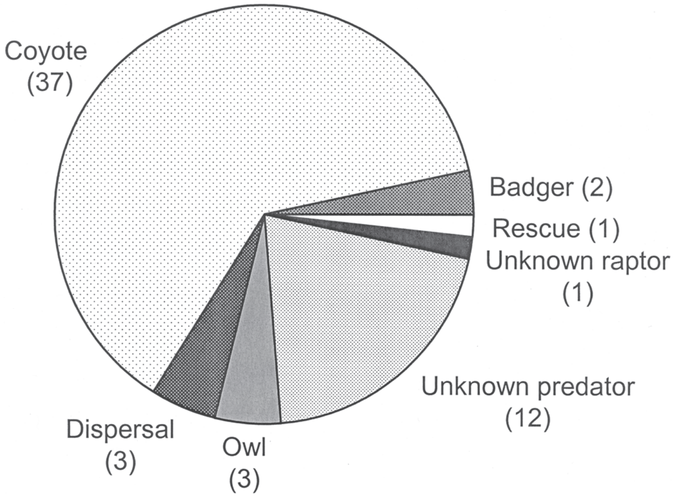

Figure 1. Causes of loss for 59 of 137 radio-tagged black-footed ferrets (*Mustela nigripes*) released in Montana, South Dakota, and Arizona during 1994–96. "Rescued" ferrets are those that we assume would have been lost without our intervention (translocation or treatment for injuries). "Unknown predator" 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.

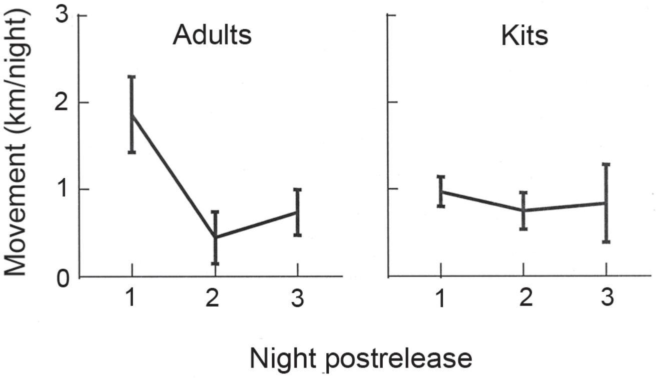

Figure 2. Mean cumulative nightly movements for adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) during the first three nights postrelease (mean ± SE).

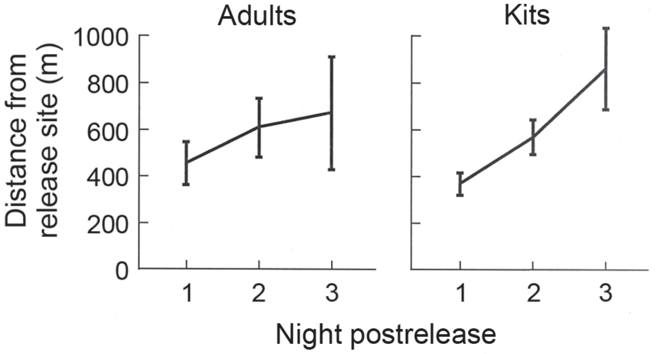

Figure 3. Nightly maximum displacement from release sites for young and adult radio-tagged black-footed ferrets (*Mustela nigripes*) during the first three nights postrelease (mean ± SE).

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

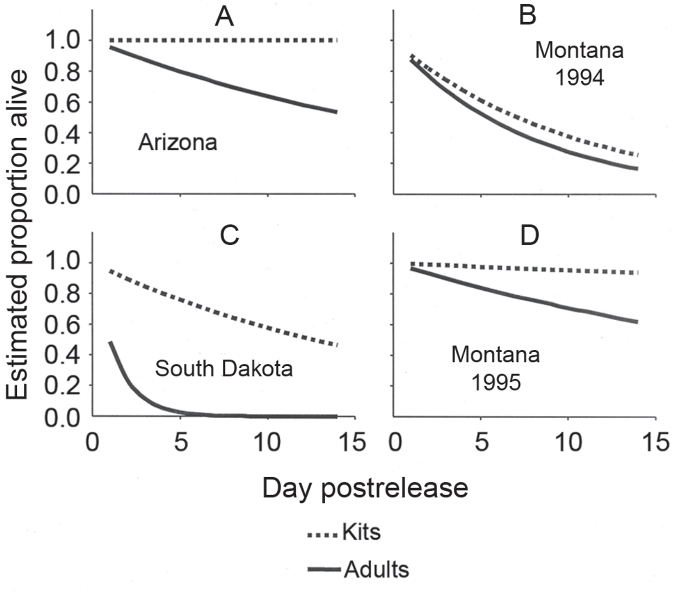

Figure 4. Postrelease survival curves for preconditioned adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) extrapolated from daily survival rates (assuming a constant hazard rate for the 14-day period of the experiment and using only known deaths).

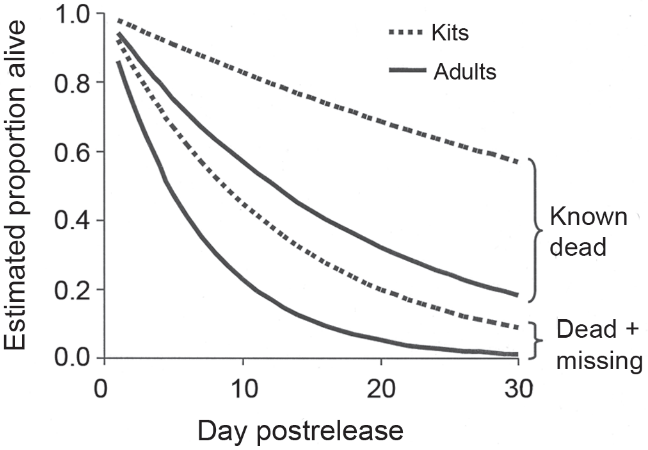

Figure 5. Bracketed high and low survival of adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) for the first 30 days postrelease, generated by using only ferrets known to be dead (high) and known deaths plus ferrets lost to radio contact (low). Curves were extrapolated from daily 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.

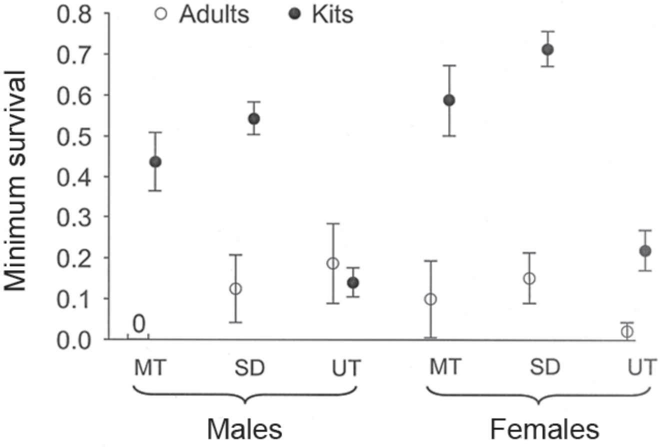

Figure 6. Minimum short-term (30-day) survival of adult and young preconditioned black-footed ferrets (*Mustela nigripes*) released onto prairie dog colonies (*Cynomys* spp.) in Montana (MT), South Dakota (SD), and Utah (UT) during 1994-2001 (mean ± SE).

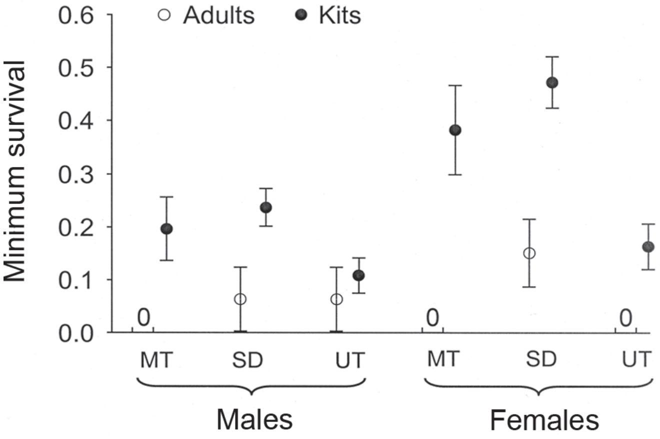

Figure 7. Minimum long-term (150-day) survival of adult and young preconditioned black-footed ferrets (*Mustela nigripes*) released onto prairie dog (*Cynomys* spp.) colonies in Montana (MT), South Dakota (SD), and Utah (UT) during 1994–2001 (mean ± SE).

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

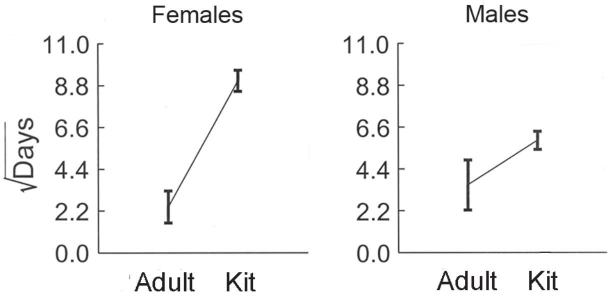

Figure 8. Number of days of known survival for marked adult and young black-footed ferrets (*Mustela nigripes*) calculated using detections from spotlight searches, snow-track searches, and radio telemetry (mean ± SE).

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 radiotelemetry 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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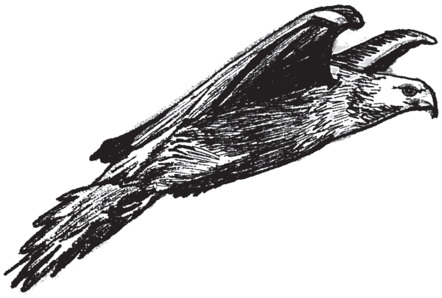

Does Predator Management Enhance Survival of Reintroduced Black-footed Ferrets?

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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

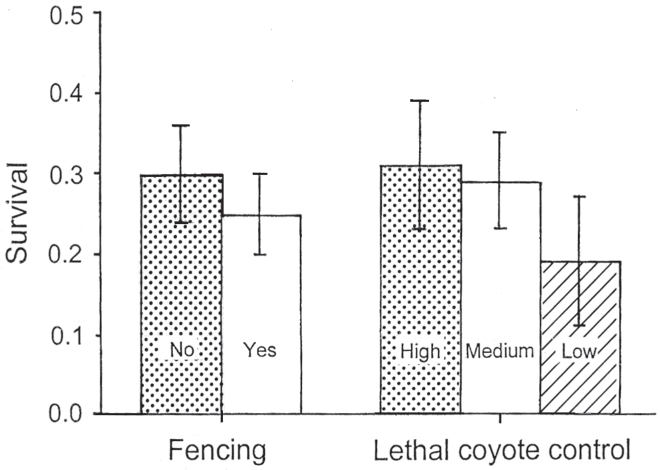

Figure 1. Estimates of short-term (1 month) minimum survival of reintroduced black-footed ferrets (*Mustela nigripes*) for two explanatory variables: fencing (present or not) and lethal coyote control (low, medium, and high). In total, 489 ferrets were released from different sites in Montana and South Dakota from 1994 to 2003. Error bars represent 95% confidence intervals.

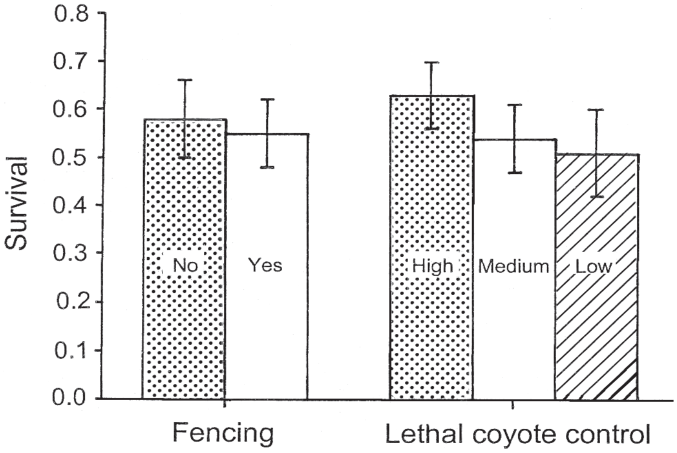

Figure 2. Estimates of long-term (6–8 months) minimum survival of reintroduced black-footed ferrets (*Mustela nigripes*) for two explanatory variables: fencing (present or not) and lethal coyote control (low, medium, and high). In total, 489 ferrets were released from different sites in Montana and South 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.

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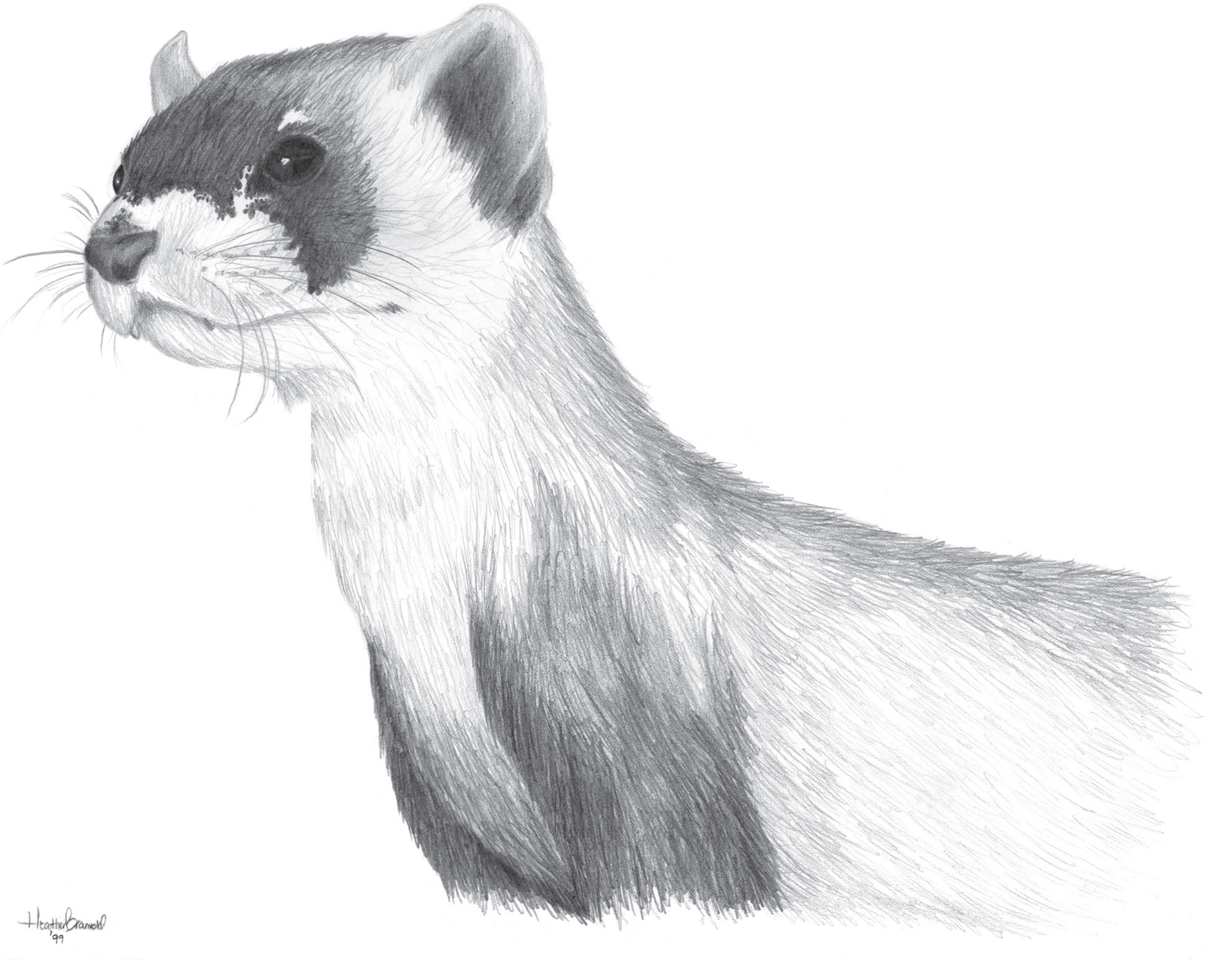
Heather Bramwell
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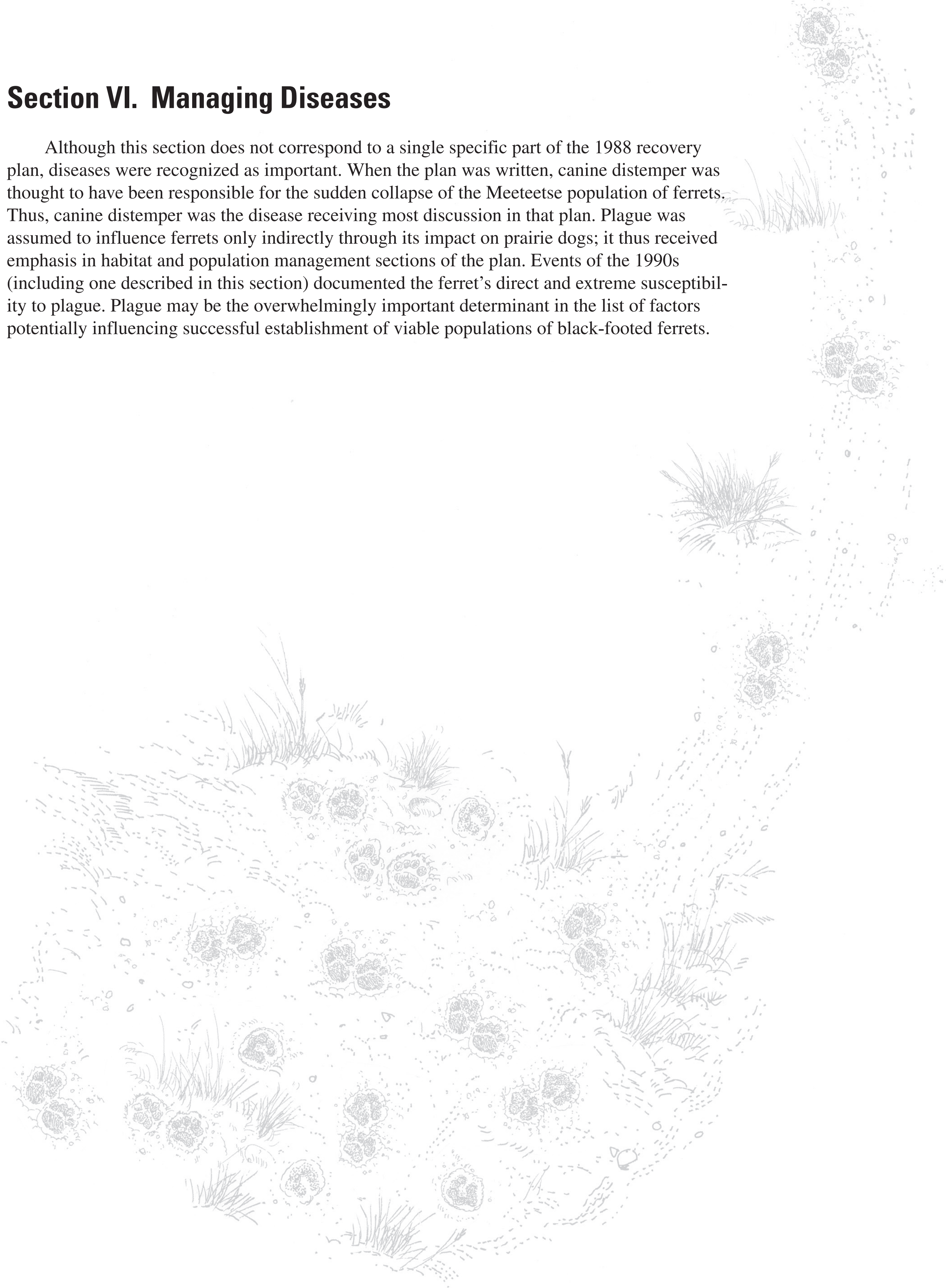
Section VI. Managing Diseases

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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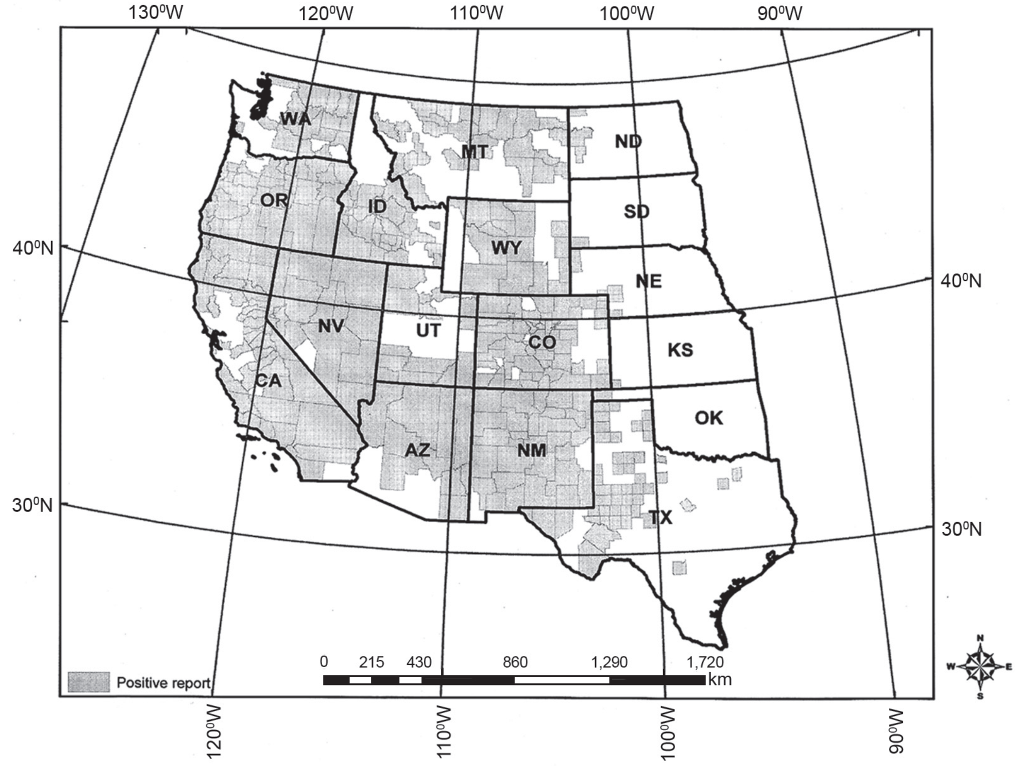

Figure 1. Counties with plague-positive mammals or fleas (1970–present). Figure courtesy of Centers for Disease Control and Prevention.

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

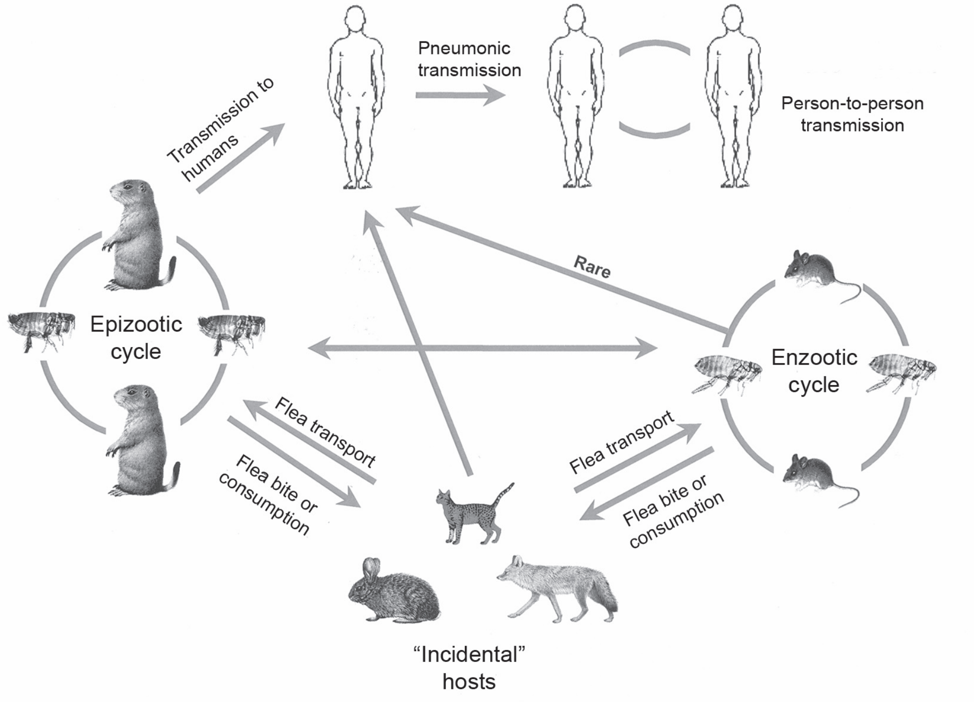

Figure 2. Generalized plague transmission cycle for the United States. Figure courtesy of Centers for Disease Control and Prevention.

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.

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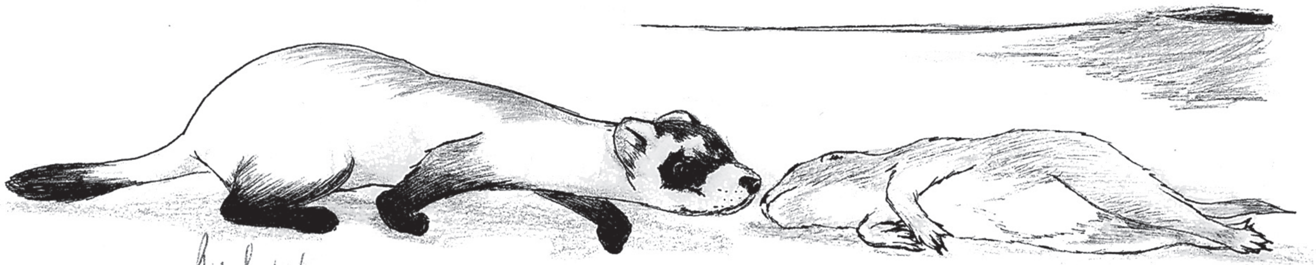

Exposure of Captive Black-footed Ferrets to Plague and Implications for Species Recovery

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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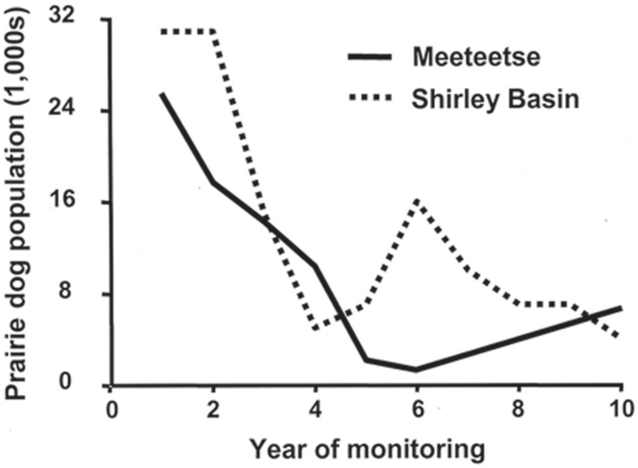

Figure 1. Changes in Wyoming white-tailed prairie dog (*Cynomys leucurus*) populations in areas with known plague. (Adapted from Biggins and Kosoy, 2001. Reprinted with permission of the *Journal of the Idaho Academy of Science*, Pocatello, Idaho.)

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

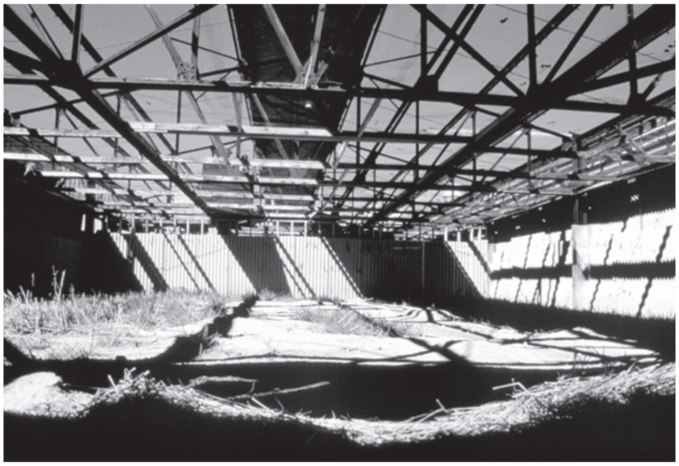

Figure 2. Black-footed ferrets (*Mustela nigripes*) occupied complex burrow systems dug by prairie dogs (*Cynomys* spp.), making them difficult or impossible to locate during and after the outbreak of plague.

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.

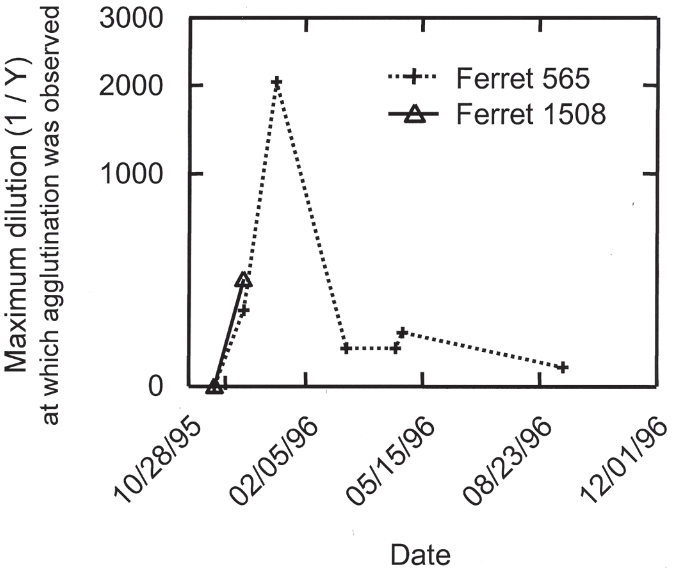

Figure 3. Antibody responses (as determined by passive hemagglutination) of black-footed ferrets (*Mustela nigripes*) #1508 and #565. Estimated date of exposure was 11/19/1995.

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.

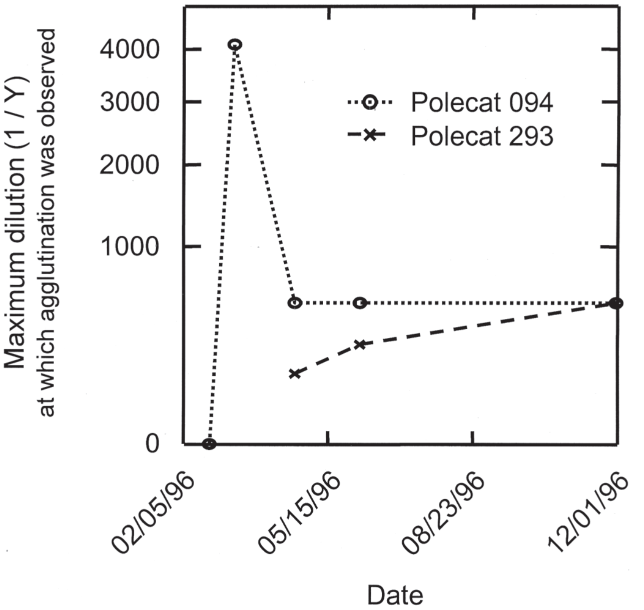

Figure 4. Antibody responses (as determined by passive hemagglutination) of two Siberian polecats (*Mustela eversmannii*) exposed to plague. Earliest potential date of exposure was 1/23/1996, when polecats were moved into pens.

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.

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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).

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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).

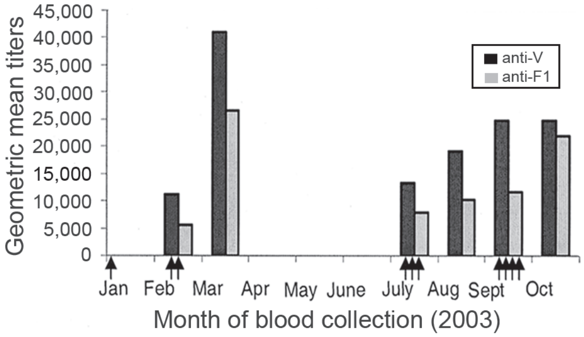

Figure 1. Geometric mean anti-F1 and anti-V antibody titers in black-footed ferrets (*Mustela nigripes*) immunized with F1-V protein. The dates of the first and second vaccinations (prime and boost), first subcutaneous challenge with *Yersinia pestis*, and second challenge via ingestion of infected mice 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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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.

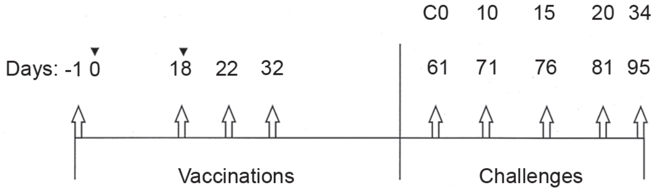

Figure 1. Timeline for the black-footed ferret (*Mustela nigripes*) Galaxy-D booster and virulent canine distemper virus challenge study. Seronegative domestic ferrets (*M. putorius furo*) in the same room served as challenge strain controls, and another cohort of pair-housed domestic ferrets had one 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.

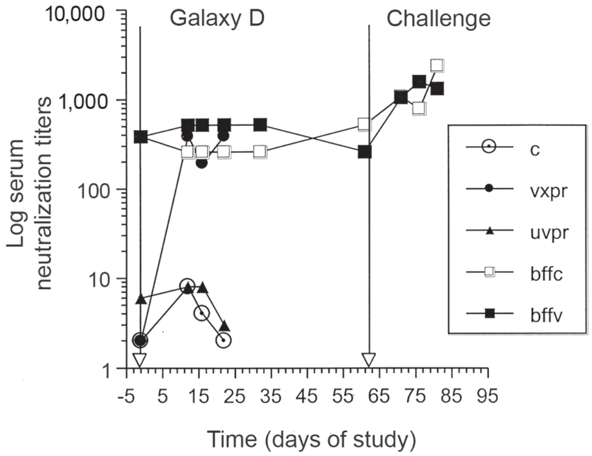

Figure 2. Serum neutralization titers for domestic ferret (*Mustela putorius furo*) controls (c), vaccinated domestic ferrets (vxpr), pair-housed unvaccinated domestic ferrets (uvpr), previously vaccinated older black-footed ferrets (*M. nigripes*) receiving Galaxy-D boostering prior to challenge (bffv), 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

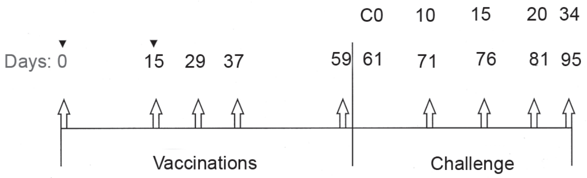

Figure 3. Timeline for canarypox-vectored recombinant canine distemper virus vaccine (reCDV) trials in Siberian polecats (*Mustela eversmannii*) and in the reCDV-Galaxy-D boostering study where the same timeline was used except that Galaxy-D was substituted for the second reCDV vaccination. Triangles indicate days of vaccination. Arrows indicate days when blood samples were drawn.

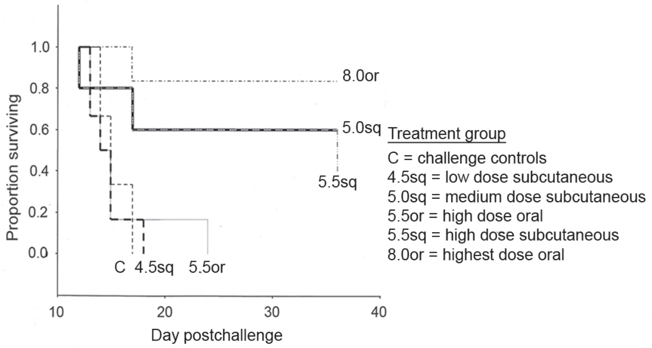

Figure 4. A survival curve is shown for canarypox-vectored recombinant canine distemper virus vaccine trials with Siberian polecats (*Mustela eversmannii*). Animals receiving two $10^{8.0}$ PFU vaccinations orally (8.0or) survived. Those receiving lower subcutaneous doses (e.g., 5.0sq) had lower survival 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*.)

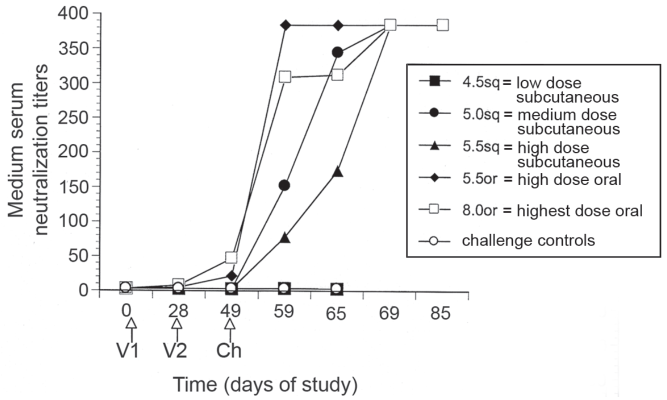

Figure 5. Serology results from the canarypox-vectored recombinant canine distemper virus (CDV) vaccine dose-response study where varied doses were administered subcutaneously or orally under isoflurane anesthesia. These results indicated that survivors mounted CDV serum neutralization titers above those 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*.)

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.

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

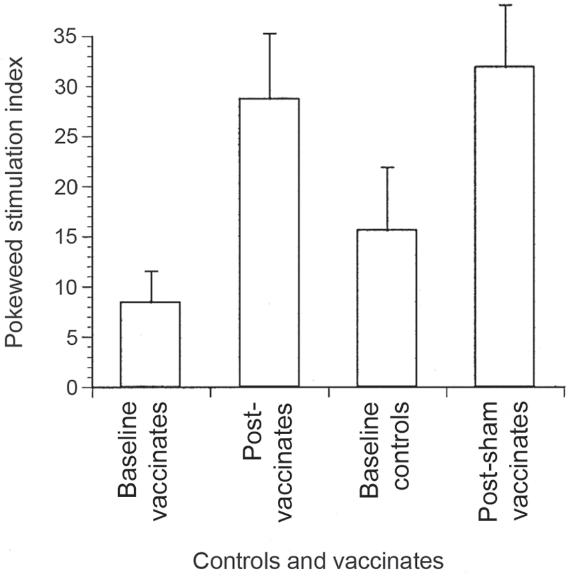

Figure 6. Pokeweed blastogenesis was performed on two samples of peripheral lymphocytes before and 14 days after canarypox-vectored recombinant canine distemper virus (reCDV) vaccination or saline control injections. The change in lymphocyte blastogenesis between controls and vaccinates was not significantly 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

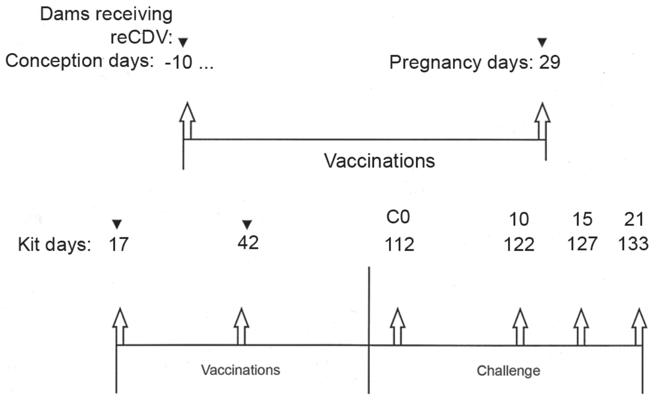

Figure 7. Timeline for the canarypox-vectored recombinant canine distemper virus (reCDV) immunization of Siberian polecat (*Mustela eversmannii*) dams to assess conception and pregnancy safety. Also shown is the timeline for vaccination of their kits in the passive immunity study. Triangles indicate 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 PureVax 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.

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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.

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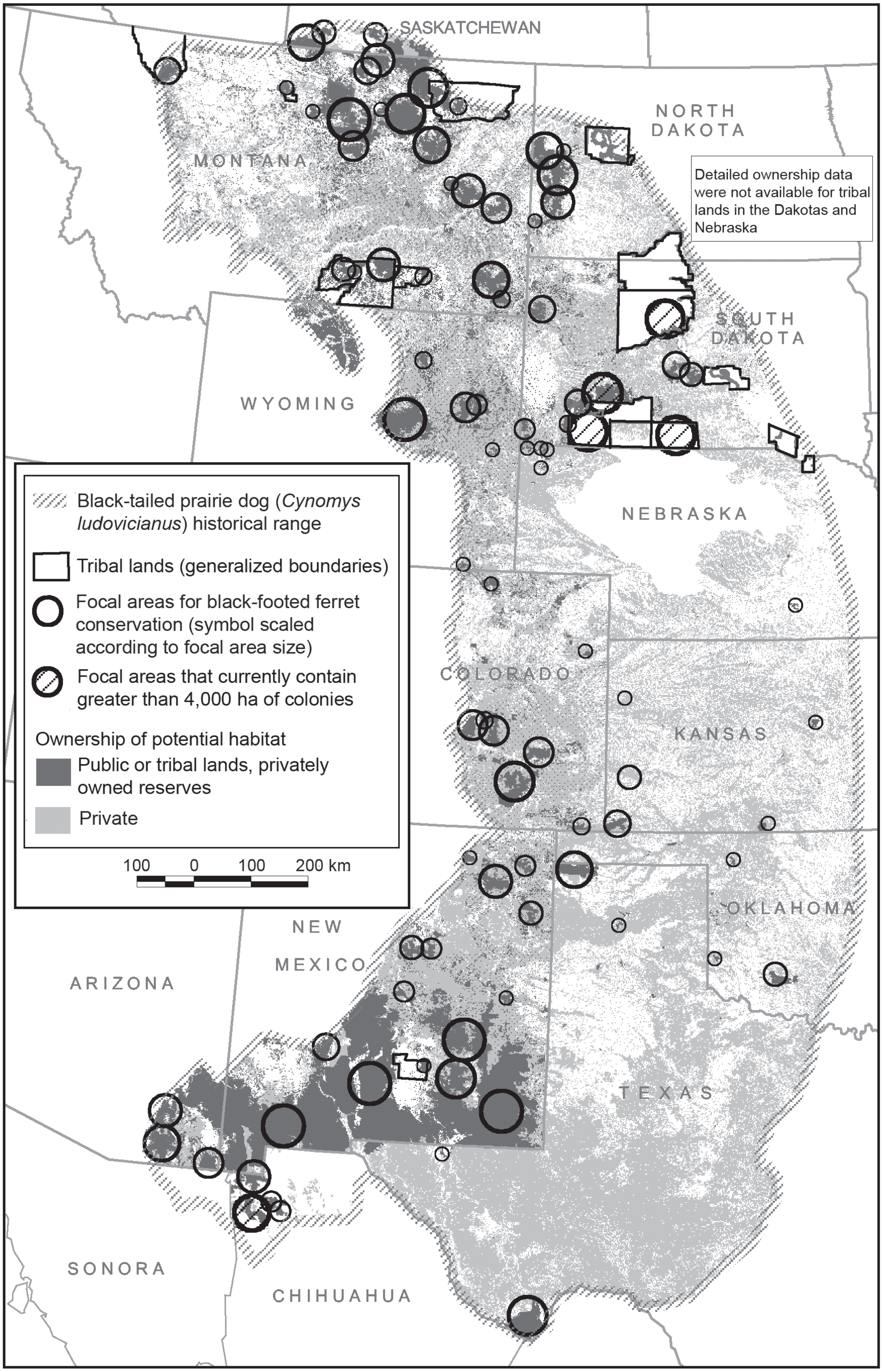

Figure 1. Focal areas for black-footed ferret (*Mustela nigripes*) recovery based on habitat suitability, land tenure, and public land contiguity.

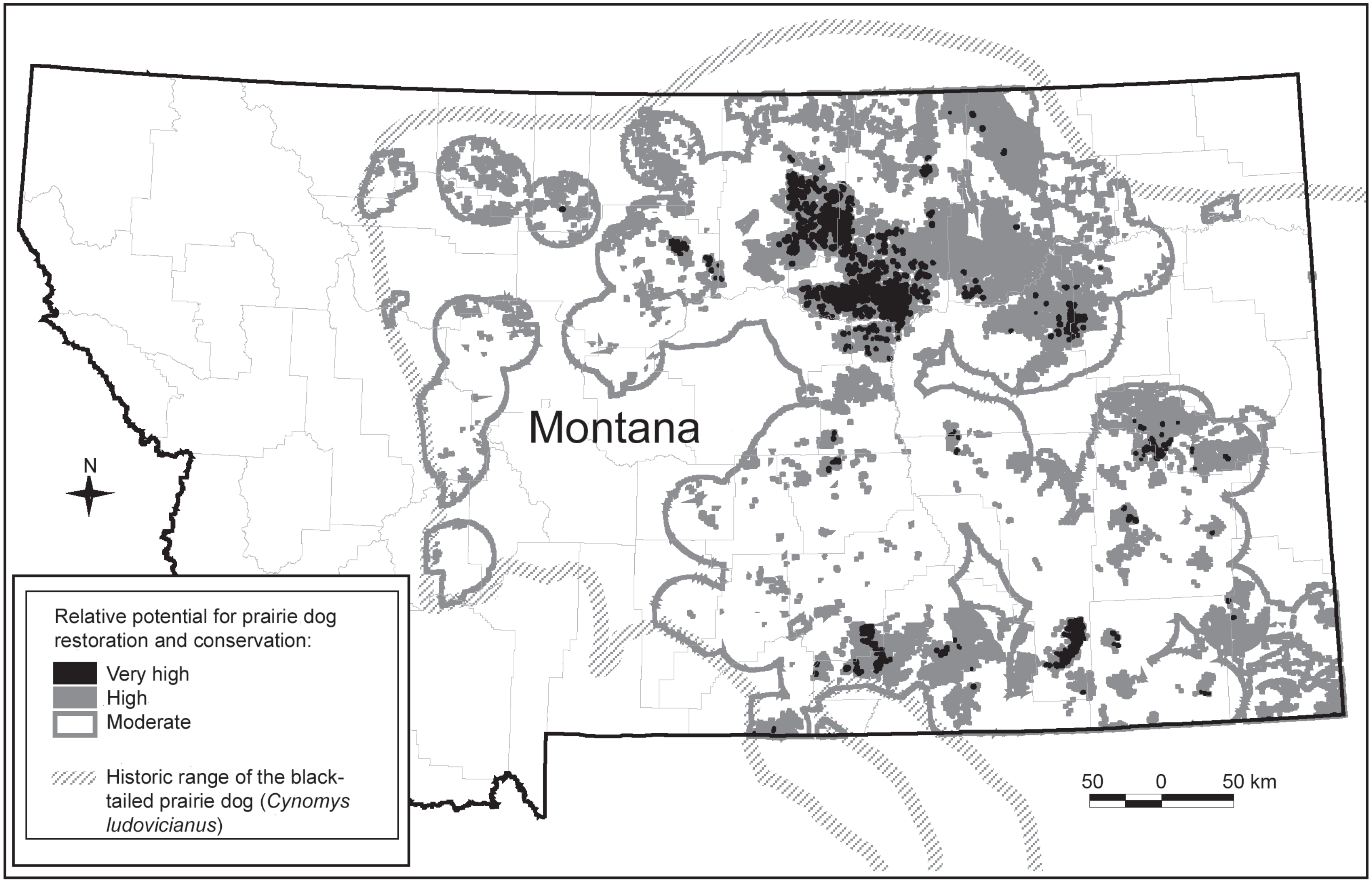

Figure 2. Relative potential for black-footed ferret (*Mustela nigripes*) recovery and restoration in Montana based on scores derived from habitat suitability, land ownership, and existing prairie dog (*Cynomys* spp.) distribution and abundance (moderate score = 1.0–2.0, high = 2.0–3.0, very high = 3.0–4.0).

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

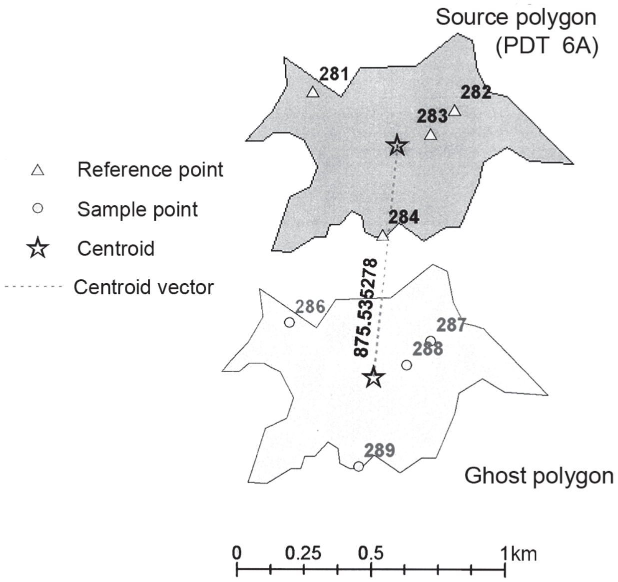

Figure 1. Generating ghost polygons and soil sample sites. Base map white-tailed prairie dog colony (*Cynomys leucurus*) PDT 6A is shown with the corresponding ghost polygon. The four soil survey sites, numbered 281–284, were selected using a randomization procedure applied to numbered cells overlaid 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

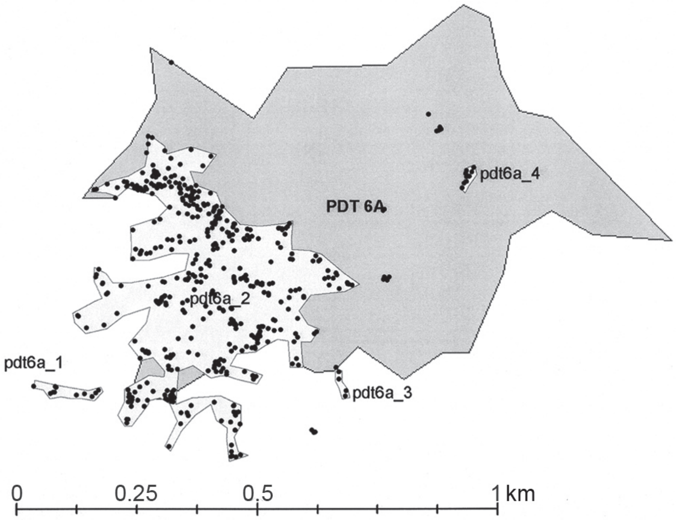

Figure 2. Trend toward fewer active burrows and contracting colony boundaries is illustrated by white-tailed prairie dog (*Cynomys leucurus*) colony PDT 6A. Active burrows recorded by GPS in early summer 2003, overlaid on the colony PDT 6A, mapped in 2001.

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.

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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.

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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.

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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

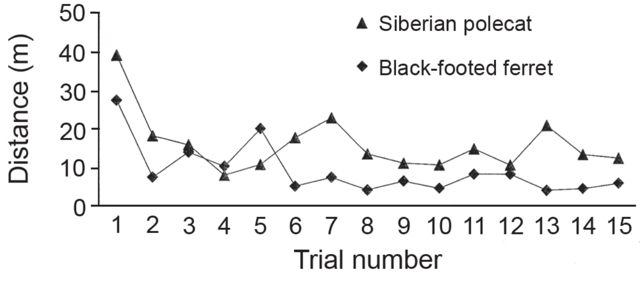

Figure 1. Mean distance traveled (m) by black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*) during 15 consecutive trials.

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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).

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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.

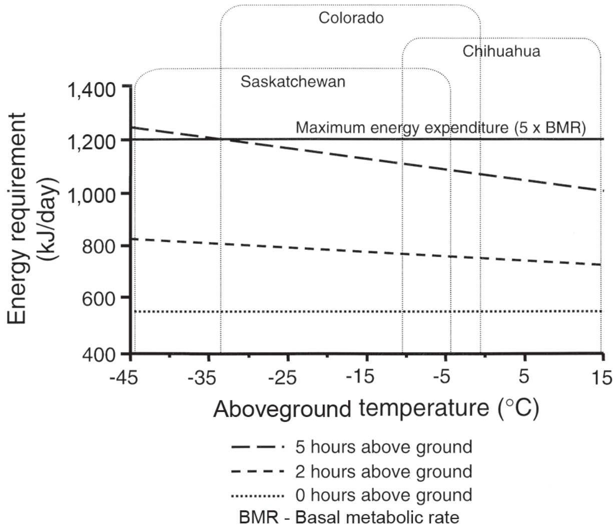

Figure 1. Predicted daily energy requirements for a black-footed ferret (*Mustela nigripes*) in winter in relation to aboveground temperature and amount of time spent above ground. Bracketing lines depict the range of winter temperatures for example sites. Activity was modeled to include mostly running 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)?

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