DISSERTATION

POPULATION ECOLOGY OF BLACK-FOOTED FERRETS (*MUSTELA NIGRIPES*) IN RELATION TO SYLVATIC PLAGUE

Submitted by

Travis M. Livieri

Department of Biology

In partial fulfillment of the requirements
For the Degree of Doctor of Philosophy
Colorado State University
Fort Collins, Colorado
Fall 2023

Doctoral Committee:

Advisor: Lisa Angeloni

Michael Antolin
Dean Biggins
Kevin Crooks

ABSTRACT

POPULATION ECOLOGY OF BLACK-FOOTED FERRETS (*MUSTELA NIGRIPES*) IN RELATION TO SYLVATIC PLAGUE

Infectious diseases can have significant impacts, both direct and indirect, on the conservation of endangered species. A full understanding of these impacts is hindered by the difficulty of teasing apart disease effects from other factors that led to endangerment, the scarcity of population data from before and after disease detection, and the inherent challenge of studying rare species, which are often difficult to detect. Ideally, a disease and population monitoring strategy will detect outbreaks so effective management and mitigation strategies can be implemented. Disease mitigation strategies, such as vaccination or removal of infected individuals, can be effective but costly to implement and rigorous evaluations of such efforts are rare. Here we present a case study and evaluation of a multi-faceted effort to manage multiple impacts of sylvatic plague (plague hereafter), an invasive disease, in a reintroduced population of endangered black-footed ferrets (*Mustela nigripes*) and their prey, black-tailed prairie dogs (*Cynomys ludovicianus*), in Conata Basin/Badlands National Park, South Dakota. Since reintroduction in 1994-1999, this is the largest free-ranging ferret population.

Chapter One provides a broad introduction to black-footed ferret natural history, ecology, and conservation efforts. We briefly described the life history of black-footed ferrets, their reliance upon prairie dogs (*Cynomys* spp.) as prey and habitat engineers, and the conflicts between prairie dogs and agricultural interests that motivated human efforts to eradicate prairie dogs and inadvertently drove ferrets towards extinction. Ensuing captive breeding and

reintroduction efforts averted extinction of the species, but plague, caused by *Yersinia pestis* bacteria, led to high mortality in both black-footed ferrets and prairie dogs, was a second factor in ferret decline, and continues to threaten reintroduced populations. Plague management, through flea vector control and vaccination, is a high priority for the black-footed ferret recovery program, along with maintaining genetic diversity and securing habitat. We concluded that black-footed ferret recovery to date has been partially successful, but challenges remain, and plague represents the largest biological threat.

In Chapter Two, we evaluated the efforts to manage plague for black-footed ferrets and prairie dogs at Conata Basin/Badlands National Park. We effectively monitored plague using carnivore serology, prairie dog testing, and visual surveys to detect the invasion of plague and inform our mitigation efforts. Both prairie dog colonies and black-footed ferret populations declined precipitously with the plague epizootic. We applied deltamethrin dust into prairie dog burrows to kill fleas and vaccinated black-footed ferrets against plague during annual monitoring efforts. Our results suggested that dusting was effective in maintaining prairie dog colonies compared to non-dusted colonies and significantly increasing survival of black-footed ferrets. Additionally, our vaccination of black-footed ferrets added incremental gains in ferret survival. These combined efforts of plague surveillance, dusting prairie dog burrows, and vaccinating black-footed ferrets likely prevented extirpation of this population.

In Chapter Three, we used stable isotope analysis to understand the effects of plague on the proportion of prairie dogs in black-footed ferret diets. Previous studies on black-footed ferrets found up to one-third of ferret diet is comprised of non-prairie dog rodents. Plague causes high mortality in prairie dogs and other small mammals found on prairie dog colonies, potentially increasing variability in prey available for black-footed ferrets. We sampled black-

footed ferrets and two prey items, prairie dogs and deer mice (*Peromyscus sonoriensis*), before and during a plague epizootic and used stable isotope analysis to estimate the diet proportions in relation to plague and dusting. We found that prior to plague black-footed ferret diets in Conata Basin/Badlands National Park were similar to previous studies, but during a plague epizootic ferrets shifted their diet almost completely to prairie dogs. Dusting prairie dog burrows prior to the invasion of plague had a similar effect in shifting black-footed ferret diets. We concluded that despite observed foraging plasticity, black-footed ferrets can be considered prairie dog colony specialists, and any diet effects following deltamethrin dust treatment are likely less severe than the impacts of plague on unprotected ferret populations.

ACKNOWLEDGMENTS

I am very grateful to my advisors and committee who supported, mentored, and inspired me throughout this degree. Mike Antolin, thank you for encouraging my nonlinear path and sharing your thoughtful perspectives on plague, prairie dogs, and black-footed ferrets. Kevin Crooks, you pushed me to think bigger, widen my perspectives, and see my black-footed ferret work in a different light. Lisa Angeloni, you were there to keep me on track, provide instant feedback, and reel me in when needed, while also making me a better writer/editor. Dean Biggins, you have been, and continue to be, an inspiration, helping to shape my progression as a biologist trying to balance science and conservation.

The black-footed ferret recovery project at Conata Basin/Badlands National Park and my dissertation research received support from US Forest Service – Wall Ranger District, Badlands National Park, US Fish and Wildlife Service, South Dakota Game, Fish and Parks (including Wildlife Diversity Grant), US Geological Survey – BRD (FORT and NWHC), USDA-APHIS, World Wildlife Fund, Defenders of Wildlife, Badlands Natural History Association, National Fish and Wildlife Foundation, The Nature Conservancy, American Ferret Association, Dakota Zoo, Smithsonian Conservation Biology Institute, Prairie Wildlife Research, and many private donors.

My co-authors in this dissertation include Steve Forrest, Randy Matchett, David Eads, Stewart Breck, Randy Griebel, Greg Schroeder, Doug Albertson, Dean Biggins, Tonie Rocke, Bill Kendall, Kevin Crooks, Lisa Angeloni, Craig Stricker, Gonzalo Barcelo, and Jon Pauli. Additionally, over the past 29 years, I have had many collaborators, supporters, partners, and friends including Bill Perry, Peter McDonald, Nancy Warren, Doug Sargent, Randy Griebel, Jeff

Abegglen, John Sidle, Greg Schenbeck, Phil Dobesh, Alex Grant, CJ Woodard, and Tony Willman (US Forest Service), Bruce Bessken, Brian Kenner, Glenn Plumb, Doug Albertson, Greg Schroeder, Eddie Childers, Dan Licht, Josh Delger, Kit Bramblee, and Paul Roghair (National Park Service), Scott Larson, Mike Lockhart, John Hughes, Paul Marinari, Randy Matchett, David Jachowski, Micah Reuber, and the staff/veterinarians at FCC (US Fish and Wildlife Service), Dean Biggins, David Eads, Patty Stevens, Tonie Rocke, and Judy Williamson (USGS), Kristy Bly (World Wildlife Fund), Jonathan Proctor and Chamois Andersen (Defenders of Wildlife), Lindsey Sterling-Krank (HSUS), Terry Lincoln and Larry Klemer (Dakota Zoo), three generations of the Godbey family, Shaun Grassel, Brent Houston, Eric Anderson, Brad Swanson, Sam Wisely, Rachel Santymire, JoGayle Howard, Silka Kempema, Eileen Dowd-Stukel, Stewart Breck, Skyla Fay, colleagues at UW-Stevens Point, and last, but certainly not least, the inimitable Steve Forrest. To anyone that I may have missed, it was not intentional, but please know that I am so grateful to have so many partners.

To my family and friends, my parents, siblings, April's parents, aunts, uncles, cousins, the Fabiszak, Suhorepetz, and Slaby families, I am so thankful for your support and encouragement in my black-footed ferret endeavors. Most importantly, I am thankful for the love, support, and patience of my wife, April, our numerous pet ferrets, and our dogs, Cleo, Watson, and Bruno.

DEDICATION

For the black-footed ferrets and prairie dogs in Conata Basin/Badlands National Park that we work so hard to conserve!

TABLE OF CONTENTS

1. CONSERVING ENDANGERED BLACK-FOOTED FERRETS: BIOLOGICAL THREATS, POLITICAL CHALLENGES, AND LESSONS LEARNED

Summary

There may be few stories in the annals of wildlife management that are as dramatic as the near demise and comeback of the black-footed ferret (*Mustela nigripes*). Endemic only to North America, this charming little carnivore found only in the continent's central grasslands was hardly known to science until the mid-20th century. By then, vast colonies of the prey it depended on for food and shelter, the prairie dog (*Cynomys* spp.), had been wiped out through disease (sylvatic plague) and an agricultural industry with little tolerance for burrowing and grazing rodents. At its low point, the species' fate would come down to 18 remaining ferrets and a scientific gamble that humans could intervene to save a species on the very brink of extinction. With heroic efforts by federal, state, and private scientists, immediate extinction was forestalled, and a comeback effort mounted. Like so many endangered species stories, the ferret's tale is a story of tragedy, luck, science, and the acts of people that will determine its ultimate fate. Understanding the challenges going forward for the ferret requires an understanding of the natural history and ecology of black-footed ferrets and prairie dogs, diseases and disease management, and the political landscape, which we present here. The future for black-footed ferrets remains unclear. Ultimately we will need to summon the efforts of conservation biologists, policy makers, and the agricultural industry to determine if ferrets will continue to exist as a valued and unique part of North America's natural heritage.

Natural history

Black-footed ferrets (*Mustela nigripes*) are small, sinuous carnivores in the weasel family (Mustelidae, sub-family Mustelinae), whose closest relatives include Siberian polecats (*M. eversmanii*) and European polecats (*M. putorius*) (Anderson et al. 1986). Their fur is black on the lower legs, feet, and tail tip in addition to a black mask, but most of the body is tan with black-tipped hairs along the back and lighter coloration on the underside (Figure 1.1). The fur is approximately 1 cm long throughout the year without any seasonal change in color. Adult body length of black-footed ferrets is 35–45 cm plus a 12 cm tail and body weight of 550–1340 g. Black-footed ferrets are sexually dimorphic with females 93% of body length and 68% of body weight of males (Anderson et al. 1986).

Ancestral black-footed ferrets are thought to have entered North America from Asia during the Pleistocene (approximately 600,000 years before present) and are the only ferret species native to the continent (Koepfli et al. 2008). Initially generalist predators, North America's ferrets evolved to become specialists on colonial, burrowing prairie dogs (Rodentia:Sciuridae; *Cynomys* spp.). The range of black-footed ferrets has an approximate 30–50 degrees extent in latitude and coincides with the collective ranges of three prairie dog species (Figure 1.2): black-tailed (*C. ludovicianus*; Figure 1.3), white-tailed (*C. leucurus*), and Gunnison's (*C. gunnisoni*). The relationship that developed makes black-footed ferrets obligate predators, dependent upon prairie dogs as prey and prairie dog colonies and burrow systems for habitat.

Black-footed ferrets are polygynous breeders and largely solitary as adults. Adult females are induced ovulators, with eggs available for fertilization only after copulation. Breeding occurs underground during March-April with a 42-day gestation period. Females whelp kits during

May-June and provision young with milk for 30–40 days, later feeding their kits prey, primarily prairie dogs. Kits generally first emerge above ground in early summer at 50–60 days of age. Female black-footed ferrets are often observed with 2–3 kits, on average, but litter counts can be up to 7 in the wild and 10 in captivity (Biggins and Eads 2017, Eads and Marsh 2020). Kits become increasingly independent in late August through September when they reach adult size and begin dispersal from their natal territories.

Black-footed ferrets are considered adults during their first winter. On black-tailed prairie dog habitat (Figure 1.4), adult male ferrets use home ranges (~130 ha) that are about 2-times larger than, and spatially overlap, those of adult females (65 ha; Livieri and Anderson 2012). Like other mustelids, black-footed ferrets are territorial, with males prioritizing access to females and females selecting for resources (Powell 1979, Biggins et al. 2006, Eads et al. 2014). In particular, adults concentrate their activities in areas with relatively high densities of active prairie dog burrow openings, thus providing them not only with numerous escape routes from predators, but also relatively high prey densities (Eads et al. 2011, Livieri and Anderson 2012).

The average life span of wild-born black-footed ferrets is approximately 1 year (Biggins and Eads 2017), though individuals up to 5 years old have been observed. Predation and disease are important sources of mortality. Coyotes (*Canis latrans*) appear to be the primary predator of black-footed ferrets and have accounted for 67% (49/73) of recorded predation events on radio-collared ferrets (Biggins et al. 2006, Biggins and Eads 2017). In some cases, American badgers (*Taxidea taxus*) and great horned owls (*Bubo virginianus*) also contribute to ferret losses. Plague, a non-native disease, can be particularly devastating because it is highly fatal in both black-footed ferrets and prairie dogs, thus having multiple effects on black-footed ferrets and efforts to conserve them (Eads and Biggins 2015, Biggins and Eads 2017).

Black-footed ferrets hunt mostly at night, when prairie dogs are sleeping in their burrows with close kin. A kill is typically made underground by rousing a prairie dog to expose its throat and applying a suffocation bite. The black-footed ferret's elongated body and ability to twist and turn in 10 cm-wide tunnels is well-suited for leverage against the tunnel walls while subduing the intended victim that may outweigh the ferret. Other hunting strategies include early morning ambush attacks (Eads et al. 2010), although prairie dogs may be more aggressive and thwart black-footed ferret attacks during the day (Livieri et al. 2013). Black-footed ferret scats contain prairie dog hair, bones, claws, and paws, suggesting they consume most or all of a prairie dog. While ~75% of black-footed ferret assimilated diets are prairie dogs, they will opportunistically prey upon other available species like ground squirrels, mice, voles, and rabbits that occur on prairie dog colonies (Henderson et al. 1969, Sheets et al. 1972, Campbell et al. 1987, Brickner et al. 2014, Tretten 2019). While this foraging "plasticity" may suggest a broader range of habitat and prey (Owen et al. 2000, Fox et al. 2017), it is clear that black-footed ferrets can only survive by living in the tunnel systems and preying on the prairie dogs that create and maintain that unique underground habitat (Anderson et al. 1986, Biggins et al. 2006). Without large, healthy, and intact prairie dog ecosystems, the fate of wild populations of black-footed ferrets is bleak.

The near-extinction and rediscovery

Black-footed ferrets were first described to science in 1851 from a single specimen obtained in, what is now, Wyoming, but many questioned the new species for nearly a half century until additional specimens were verified (Audubon and Bachman 1851, Coues 1877). Naturalists noted early on the black-footed ferret's association with prairie dogs and suggested that ferrets were not rare, but rather elusive due to their fossorial, and as later discovered, primarily nocturnal habits. By the early 1900s, as western lands were settled in the United States (US), intensifying agriculture increasingly displaced or altered prairie dog habitat. In more fertile soils, the grasslands were converted to croplands, making them inhospitable to prairie dogs. Where intact grasslands remained, livestock producers generally maintained a negative view toward prairie dogs as grazers competing with livestock for grass (Miller et al. 2007). This concern drove demand for large-scale poisoning campaigns carried out at all levels of government in the US and Canadian portion of the range. In particular, federal programs were responsible for poisoning millions of hectares from 1916 to 1945 throughout the 12 states within the prairie dog's historical range (Forrest and Luchsinger 2006). The resulting declines in prairie dogs, and thus black-footed ferrets, were catastrophic. For example, a poisoning campaign in South Dakota from 1932 to 1939 treated more than 400,000 ha total in all counties within the prairie dog range with reported eradication of prairie dogs in 30 of 34 counties. In Kansas, there were an estimated 800,000–1,000,000 ha of prairie dog colonies statewide in the early 1900s (Lantz 1903), but by the 1970s only 14,526 ha remained, a reduction of 98% (Anderson et al. 1986).

To add further stress on this ecosystem, a lethal bacterial pathogen, plague (*Yersinia pestis*), became established in parts of the prairie dog range during this same period. The bacterium was unintentionally introduced to California in the early 1900s, arriving in infected fleas and rats aboard Asian trading ships. It spread quickly, expanding >2,000 km eastward in only 60 years and overtaking a significant portion of the prairie dog and black-footed ferret range (Figure 1.2). Plague continued to expand eastward, and now encompasses nearly the entire historical range of black-footed ferrets (Miller and Reading 2012). Epizootic outbreaks of plague, relatively short but explosive events with high transmission rates lasting from a few months to years, often result in near total elimination of affected prairie dog colonies.

The effects of poisoning, exacerbated by plague, resulted in a highly fragmented mosaic of distantly separated prairie dog colony "islands," which in turn isolated remaining clusters of black-footed ferrets across the range and greatly increased the probability of extirpation for each remaining population. Black-footed ferrets dwindled in distribution and population size rapidly and after 1937 were no longer observed in Arizona, Utah, Oklahoma, Texas, and Saskatchewan. By 1957 the last black-footed ferrets occupying New Mexico, Colorado, Kansas, Nebraska, and North Dakota were reported (Anderson et al. 1986). By this time, the species was widely recognized as imperiled and calls for conservation and biological studies were increasing (Cahalane 1954, Garst 1954). A population of black-footed ferrets discovered on private lands in Mellette County, in southcentral South Dakota in 1964, provided not only the first insights into life history, behavior, and survey methodology, but also renewed calls for conservation action (Hillman 1968, Henderson et al. 1969). The United States Fish and Wildlife Service (USFWS) established an endangered species research program at Patuxent National Wildlife Refuge, Maryland in 1965 to attempt captive propagation of a handful of endangered species, including the black-footed ferret. The black-footed ferret was one of the first species listed as endangered by the International Union for the Conservation of Nature (IUCN) in 1966 and by the USFWS under the Endangered Species Preservation Act of 1966, the precursor to the Endangered Species Act of 1973.

Six black-footed ferrets were captured from Mellette County in 1971 and transported to Patuxent. Four died of vaccine-induced canine distemper virus when they were prophylactically administered a modified-live vaccine that was safe for domestic ferrets (*M. p. furo*), providing a first harsh lesson in the complexities of captive propagation and the importance of disease management for ferrets (Carpenter et al. 1976). Three more black-footed ferrets were captured to bring the potential captive breeding population up to five individuals. Although two litters were produced, none of the kits survived (Hillman and Carpenter 1984). In the wild, the Mellette County population was extirpated by 1974, presumably due to continued prairie dog poisoning, and, despite reward programs and active searches, no additional wild populations were located (Hanebury and Biggins 2006). The USFWS wrote a black-footed ferret recovery plan in 1978, but it appeared to be too late for effective conservation. The last of the captive Patuxent black-footed ferrets died in 1979 (Carpenter et al. 1980) and many feared the species was now extinct (Hanebury and Biggins 2006).

Hope was restored when a ranch dog named Shep, owned by John and Lucille Hogg, killed a black-footed ferret on the night of September 26, 1981 near Meeteetse, Wyoming. This serendipitous event led to the discovery of an extant black-footed ferret population living on 2,800 ha of white-tailed prairie dog colonies scattered over private and public lands (Clark 1989). The Meeteetse black-footed ferret population, while small in size, appeared to be stable with a maximum of 129 individuals estimated in 1984 (Forrest et al. 1988). Field teams, composed of Biota Research in partnership with the USFWS, advanced the knowledge of black-footed ferret ecology, conservation needs, and enhanced research techniques during a period of high uncertainty and interagency infighting (Lockhart et al. 2006). After 2 years of field demographic studies, researchers believed the population could withstand removal of a small number of individuals for captive breeding, consistent with the best practices of the time. However, a controversial decision by USFWS ceding management authority over black-footed ferrets, a federally listed species, to Wyoming Game and Fish Department (WGFD) led to some degree of paralysis early on and delayed some critical steps advocated by outside groups, such as initiation of a captive breeding program. For its part, WGFD was hesitant because funding sources were unclear, current facilities were inadequate, and it was believed the population might be adversely affected (Lockhart et al. 2006).

Unfortunately, events overtook ongoing debate. During the summer of 1985, an epizootic of plague initially raised the alarm for managers. Large portions of prairie dog colonies suddenly became inactive and a plague-infected dead prairie dog was confirmed. The Meeteetse black-footed ferret population declined by ~50% to an estimated 58 individuals (Forrest et al. 1988). The inability to produce viable captive black-footed ferret kits from the Patuxent breeding effort a decade earlier loomed large over the remaining, and dwindling, Meeteetse ferret population. The plummeting numbers supplied the impetus to advance plans for attempting a captive population. Six black-footed ferrets were captured in fall of 1985 and transferred to a recently converted WGFD facility. Shockingly, all died within days from canine distemper virus, likely contracted in the wild. With literally the existence of the entire species in the balance, there was little choice but to attempt an expedited removal of all remaining individuals from the wild. Six more black-footed ferrets were captured from Meeteetse in October and placed in quarantine, leaving four known ferrets in the wild over the winter of 1985–86. Captive breeding in 1986 was unsuccessful, but two litters were born in the wild (Clark 1987) and by early 1987 biologists captured the last remaining 12 free-ranging black-footed ferrets for captive breeding. The entirety of *M. nigripes*, a species that once spanned 12 US states and portions of southern Canada and northern Mexico, was now 18 individuals in captivity, most with familial relationships, from one population, and on the periphery of the historical range.

Back from the abyss

The completion of a new black-footed ferret captive breeding facility in Sybille Canyon, Wyoming, along with lessons learned from the Patuxent breeding efforts, facilitated a tentative, but successful captive breeding season in 1987. WGFD led the captive breeding efforts and research, eventually distributing black-footed ferrets to six other facilities in North America to minimize the risk of holding and breeding all the remaining animals at a single facility (Lockhart et al. 2006).

The limited genetic diversity of the 18 black-footed ferret founders prompted careful breeding strategies. Much was learned about nutrition, disease management, and reproductive health (Marinari and Kreeger 2006). During this period, the USFWS began preparing for the hopeful return of black-footed ferrets to the wild by intensively studying pre-release conditioning and release techniques (Biggins et al. 1998, Biggins et al. 1999, Biggins and Eads 2017; Figure 1.5). A revised recovery plan, completed in 1988, guided the breeding program and reintroduction efforts. In 1991, four years after the last individuals were removed from the wild, the first black-footed ferrets produced in captivity were reintroduced into the wild, a remarkable success after the species was nearly extinct. Captive breeding to maintain the essential population and to support reintroduction efforts continues today (Table 1.1). The USFWS worked closely with WGFD, and many other partners, to reassume primary control of the recovery program in 1996.

An international organization of federal, state, tribal, and non-governmental entities, known as Black-Footed Ferret Recovery Implementation Team (BFFRIT), advises the USFWS on recovery activities (Lockhart et al. 2006, Jachowski and Lockhart 2009). Coordinated captive breeding efforts now occur at five zoos, including the Toronto Zoo, Phoenix Zoo, Cheyenne

Mountain Zoo, Louisville Zoo, and Smithsonian's National Zoo & Conservation Biology Institute, in addition to the National Black-Footed Ferret Conservation Center operated by the USFWS (Figure 1.6). Captive breeding and reintroduction of black-footed ferrets has faced both biological and social challenges. Guided by adaptive management, early releases of black-footed ferrets were often paired with hypothesis-driven learning objectives to improve reintroduction success. To a large degree, the technical challenges of ensuring ferrets persist following reintroduction have been mostly met.

The social challenges have proven more daunting. In some states, prairie dogs are regarded as varmints or pests, often with legal obligations to limit or eliminate them, and afforded very little protection from poisoning, shooting, land conversion, or plague (Miller and Reading 2012). Throughout the range of black-footed ferrets there are lands under various jurisdictions containing prairie dog colonies that may be suitable for reintroduction, and even some federal lands that have regulatory obligations to conserve them, but securing sufficiently large areas for ferret conservation has proven difficult. The livestock industry generally opposes large areas of prairie dog colonies that are needed to support viable populations of black-footed ferrets. Even where wildlife conservation is a priority and in protected areas, prairie dogs are still persecuted and plague remains a persistent threat (Miller et al. 2007, Miller and Reading 2012). Institutional support may be lacking, in some cases, to promote protection or restoration of prairie dog colonies. Some state wildlife agencies are highly involved and engaged in black-footed ferret reintroduction and actively manage reintroduction sites (e.g., habitat mapping, post-release monitoring, plague management), but other states, due to strong livestock industry political influence, are sometimes limited by policy or regulation from participating.

The result is that all but three of the 28 reintroduction sites to date (Table 1.1) have yet to establish self-sustaining black-footed ferret populations that persist without supplementation of additional captive-born animals (U.S. Fish and Wildlife Service 2019). Many black-footed ferret reintroduction sites are inactive because of devastating plague epizootics that eliminated habitat, or due to a collapse in political/economic support. Despite these setbacks, reintroduction sites serve as important natural laboratories for experimentation and learning where perseverance can pay off by demonstrating the potential of wild ferret populations. For instance, the reintroduced black-footed ferret populations at Shirley Basin, Wyoming and Aubrey Valley, Arizona (Figure 1.2, Table 1.1) initially were unable to establish self-sustaining populations, but continued efforts resulted in ferret populations exhibiting rapid population growth 15–16 years after the inaugural reintroductions (Grenier et al. 2007, Wisely et al. 2008).

Black-footed ferret recovery has progressed significantly since the last 18 individuals were removed from the re-discovered, and last remaining wild population near Meeteetse, Wyoming in 1987 and used to establish a successful captive breeding program. Nearly 10,000 black-footed ferrets have been born in captivity since then. Six facilities housing ~275 black-footed ferrets annually now produce 100–200 kits each year for reintroduction, in addition to maintaining the essential captive population.

More than 5,100 black-footed ferrets have been released at 28 sites in 8 US states, Mexico, and Canada (Table 1.1). Additionally, translocation of wild-born kits has been used to start new sites or supplement existing sites (Biggins et al. 2011). In 2016, after 29 years of absence, black-footed ferrets were returned to the wild near Meeteetse, Wyoming. This species has been brought back from the abyss of extinction by securing captive breeding, experimenting with reintroduction techniques, and substantial efforts to mitigate the devastating effects of plague. The next step for the black-footed ferret program is to realize full recovery of the species, a task that will require overcoming more hurdles.

The challenge of Black Death

Plague, caused by the flea-borne bacterium *Yersinia pestis*, originated 15,000–22,000 years ago in Asia and is best known for killing hundreds of millions of people during the Black Death, a devastating pandemic that peaked during the mid-1300s in Europe (Achtman et al. 1999). Plague also impacts a wide variety of wildlife directly and indirectly, primarily via lethal impacts on rodents and lagomorphs (Antolin et al. 2002, Eads and Biggins 2015). In Asian ecosystems where animals evolved with plague, the disease plays a role in the cyclic dynamics of mammal populations. However, in naïve ecosystems like North America, plague can be particularly disruptive (Biggins and Kosoy 2001). The importance of plague in black-footed ferret conservation cannot be overstated. Put simply, plague is so lethal that it functions as a unique type of predator of both prairie dogs and black-footed ferrets, posing a multi-faceted and daunting challenge for ferret recovery (Biggins and Eads 2017).

As devastating as epizootic plague can be to prairie dog populations, during inter-epizootic time periods, termed enzootic plague, transmission is dampened and the impacts are subtle, but nonetheless ecologically important, even though significant mortality can be difficult to detect (Matchett et al. 2010). Epizootic and enzootic plague can limit prairie dogs to small, scattered fragments of occupied areas that are incapable of supporting black-footed ferret populations. Furthermore, ferrets themselves are directly susceptible to plague throughout the continuum of plague transmission from low, enzootic smoldering states to epizootic eruption.

It wasn’t until the 1990s that the full extent of the threat plague poses to black-footed ferrets was wholly realized. Because domestic ferrets can be fairly resistant to plague, it was mistakenly assumed that black-footed ferrets would also have some level of inherent resistance (Williams et al. 1991). During the precipitous decline of prairie dogs from plague epizootics from 1985 to 1987 at Meeteetse, the black-footed ferret population simultaneously crashed. The best science at the time assumed the cause was related to habitat loss (i.e., prairie dog colonies) and canine distemper virus and not a direct impact of plague. Later in 1993, researchers documented fatal plague in a captive black-footed ferret (Williams et al. 1994). Then in 1995, 27 of 30 captive black-footed ferrets died within days after accidental exposure to plague-infected meat, including some that ate only surface-contaminated meat, suggesting that even low doses of the bacteria can be fatal (Godbey et al. 2006). It is now well accepted that black-footed ferrets are highly susceptible to plague, can be infected by flea bites, and by consuming infectious prey or carrion.

The combined impacts of plague on prairie dogs and black-footed ferrets can be devastating. For example, at Conata Basin/Badlands National Park in South Dakota (Figure 1.2, Table 1.1), a plague epizootic among black-tailed prairie dogs reduced approximately 14,000 ha of habitat by 73% and the population of black-footed ferrets declined from 355 to 49 in 5 years. The efforts of multiple agencies and non-governmental organizations prevented extirpation of that population through flea vector control and direct vaccination of black-footed ferrets to preserve about 4,000 ha of black-tailed prairie dog colonies at a cost of more than $200,000 annually. A study in Montana, during a period of enzootic plague, found either flea control or vaccinating black-footed ferrets against plague significantly increased their survival rates (Matchett et al. 2010). Neither prairie dogs nor black-footed ferrets have evolved immune responses sufficient to limit severe population reductions caused by plague. Unfortunately, invasive plague is persistent and relentless. The disease will play a continued, critical role in black-footed ferret conservation.

The future

Recovery of black-footed ferrets ultimately requires resilient wild populations that display a breadth of ecological and genetic diversity across its historical range (U. S. Fish and Wildlife Service 2019). Currently, the total number of breeding adult black-footed ferrets in the wild is approximately 10% of the down-listing goal of 1500 breeding adults and 5% of the 3000-adult de-listing goal. Clearly there is much work to be done and keys to recovery will involve three main elements: (1) maintaining and restoring genetic diversity with continued improvements in captive breeding (Marinari and Kreeger 2006, Wisely et al. 2015); (2) securing multiple areas where resilient black-footed ferret populations are protected, and managers are allowed and supported to protect and maintain functioning prairie dog habitat (Lockhart et al. 2006); and (3) advancing our knowledge and tools for managing plague (Biggins and Eads 2017).

Captive breeding and genetic diversity

In the near term, captive breeding will remain important in black-footed ferret conservation by providing animals for continued reintroduction efforts and maintaining genetic diversity in the relatively secure captive population (U. S. Fish and Wildlife Service 2019). Research has shown the survival of reintroduced black-footed ferrets is improved through pre-release conditioning of captive-born black-footed ferrets (Biggins et al. 1998, 1999, 2011, Biggins and Eads 2017). Standard operating procedures for black-footed ferrets destined for release now include 30–45 days in quasi-natural outdoor pens with burrows and live prey to enhance their innate skills at killing prairie dogs and avoiding predation. Pre-release conditioning occurs at the National Black-Footed Ferret Conservation Center in Carr, Colorado (Figure 1.5). Maintaining this captive breeding program with pre-conditioning pens will continue to be vital for black-footed ferret recovery.

Another important role of captive breeding is to maintain genetic diversity which is critical for minimizing potential effects of inbreeding (Santymire et al. 2019) and providing the long-term adaptive potential needed for future environmental challenges. The near extinction of black-footed ferrets severely restricted the genetic diversity of the species such that careful breeding is essential to minimize the loss of genetic diversity. A primary goal is to optimize genetic management and the captive breeding program successfully maintained >80% of the genetic diversity present in the founder population. However, long-term captive breeding is not ideal and the limitations could be overcome if sufficient habitat existed for wild propagation. For example, whelping rates in captivity have declined >50% over the past 26 years, from 75% to 35% (U. S. Fish and Wildlife Service 2019), but reintroduced wild populations maintain high whelping rates near 90% annually. Understanding and altering this pattern is an important priority for the captive breeding program. Nonetheless, given the rates of habitat restoration and protection to date because of social intolerance for prairie dogs, combined with the challenges of mitigating plague, a productive captive population of black-footed ferrets will remain essential.

Whether bred in captivity or in the wild, black-footed ferret genetic diversity will continue to slowly decline over time, thus it is important that the recovery program also finds ways to increase genetic diversity of black-footed ferrets. Recently, the USFWS and partners announced the birth of the first cloned black-footed ferret utilizing cryopreserved cells from a decades-deceased wild ferret that was no longer genetically represented in the extant population (Wisely et al. 2015). In addition to cloning, the advent of CRISPR-Cas9 genetic editing tools could replace and express genes for an increased immune response to plague (Novak et al. 2018), thus reducing the impact of this devastating disease, or restore genetic diversity with alleles from unrepresented populations (e.g., the 1960s Mellette County, South Dakota black-footed ferrets). These technologies are in early stages of development and, if successful, may be hailed as great steps forward in conservation science. Gene banking and cryopreserving materials from contemporary ferrets is being considered to safeguard against any catastrophic events that may arise in the future (U. S. Fish and Wildlife Service 2019).

Securing habitat

Black-footed ferret recovery must focus on maintaining and enhancing current recovery sites (Table 1.1) as well as restoring prairie dogs in areas for future recovery sites. The U. S. Fish and Wildlife Service (2013, p. 7) identified "the single, most feasible action that would benefit black-footed ferret recovery is to improve prairie dog conservation." However, the opposition of politically influential agricultural interests mostly prevents effective large-scale prairie dog conservation (Miller et al. 2007, Miller and Reading 2012). In the US, there are more than 163 million hectares of rangeland that are suitable for prairie dogs, yet only 1.5 million hectares (0.9%) are currently occupied by prairie dogs (U. S. Fish and Wildlife Service 2013). Black-footed ferrets currently occupy 97,197 ha of which 12,206 ha are managed for plague at some level (U. S. Fish and Wildlife Service 2019). In other words, black-footed ferrets currently occupy 0.06% of their potential range. At most, 3 sites likely had a minimum spring 2020 breeding population of 30 adults, the minimum population size to count towards recovery goals. Ten of the 28 reintroduction sites at their maximum potential size contained <2,000 ha of prairie dog colonies and have a very low probability of ever sustaining ≥30 breeding adults (Table 1.1). 18 of the 28 reintroduction sites currently have <2,000 hectares of prairie dog colonies. At the nine largest sites, current active prairie dog colony area was only ~25% of the potential or maximum size and 5 of those sites reported no known ferrets in 2019 (U. S. Fish and Wildlife Service 2019). Since 2006, only one new black-footed ferret reintroduction site has been established that contained >10,000 ha of prairie dog colonies (Table 1.1).

Increasing the number of large recovery sites will involve a consortium of federal, state, private and tribal efforts. It is becoming increasingly clear that large recovery sites will mostly occur on public and tribal lands. Private lands play an important role in black-footed ferret recovery and cooperation with landowners is essential, but prairie dog protections on private land are often difficult and sometimes ephemeral. For instance, a 1901 state law in Kansas authorizes townships to destroy prairie dogs on private lands (Lantz 1903), effectively relinquishing private property rights of any landowner with prairie dog colonies (U. S. Fish and Wildlife Service 2019). Landowner incentive programs to maintain large prairie dog colonies have only temporarily worked, in a few limited cases, and have suffered from a lack of funding and effective implementation. Native American tribes are sovereign nations with their own governments that make decisions about wildlife management. Currently, seven tribes are partnering in black-footed ferret recovery and most have the potential for large populations of prairie dogs and ferrets. Recovery sites on federal public lands, such as Conata Basin/Badlands National Park, South Dakota, are critical because these vast areas can provide the amount of habitat needed to sustain large black-footed ferret populations in addition to management stability and economic resources. That said, political complexities often make it difficult for public land managers to proactively manage for large prairie dog colonies (Miller et al. 2007). Securing habitat for black-footed ferrets is largely an issue of politics, sociology, and economics that is often beyond the purview of most biologists, thus it will require engaging with politicians, communities, and agricultural interests.

Managing plague

Any habitat that is secured for black-footed ferret recovery will likely require some level of plague management to sustain viable populations of ferrets. Currently, the most effective way of limiting the impact of plague is to use insecticides to kill fleas, the vectors of plague (Eads and Biggins 2019). This method utilizes direct application of insecticide-laden dust directly into each prairie dog burrow opening across hundreds or thousands of hectares. The active ingredient of one of the most effective insecticides is deltamethrin which causes prolonged nerve action and paralysis, thereby killing fleas that vector plague. Field studies demonstrate deltamethrin is an effective tool for protecting prairie dogs and black-footed ferrets (Biggins et al. 2010, Matchett et al. 2010), but it must be applied annually, can be costly, and fleas can develop resistance with repeated applications and under dosing (Eads et al. 2018). Recently, a systemic, orally-ingested insecticide bait containing fipronil was registered for use in prairie dogs and demonstrates effective flea control (Eads et al. 2019). Fipronil related products have the potential to be more cost effective than deltamethrin (Matchett et al. 2023) and provide an additional tool that can be rotated in an integrated plague management strategy.

Black-footed ferrets can be protected against plague using an injectable F1-V fusion protein vaccine (Rocke et al. 2008, Matchett et al. 2010). All black-footed ferrets released from captivity are routinely vaccinated before release. In the wild, black-footed ferrets are live-captured for vaccination and implantation of an identifying passive integrated transponder (PIT) tag (Figure 1.7). The vaccine is most effective with the injection of two doses, a primary and a booster, >2 weeks apart. Vaccinating wild black-footed ferrets produces protective titers against plague for individuals but their prairie dog prey and habitat remains vulnerable to plague. An experimental oral sylvatic plague vaccine (SPV) for prairie dogs was tested in four prairie dog species across seven states, providing partial protection when plague was detected (Rocke et al. 2017). Further refinements in SPV are needed as the current formulation may not provide sufficient protection to maintain high quality black-footed ferret habitat.

Currently, an integrated plague management strategy utilizing both insecticides for vector control and vaccination of black-footed ferrets is the most effective strategy to protect both species from plague. While this combined plague management strategy is costly and labor intensive, those treatments resulted in the persistence of many reintroduced wild black-footed ferret populations.

There is an urgent need to learn more about plague ecology in prairie dog ecosystems so plague mitigation can be strategized in time and space. Data suggest weather influences plague frequency. In some studies, epizootics of plague have occurred in conjunction with increased precipitation and mild temperatures, especially after periods of drought. Paltry precipitation may predispose prairie dogs to malnourishment and higher rates of flea parasitism that may increase plague transmission rates to epizootic levels as mild, wetter patterns provide more favorable conditions for prairie dog reproduction and plague bacterium replication (Eads and Biggins 2017). Accumulating studies, from both North America and Asia, support this notion of dry conditions followed by returning rains and mild temperatures stimulating epizootic events.

Climate change may play a role in the occurrence of plague epizootics; contemporary global warming is forecasted to amplify the hydrological cycle, causing an increased occurrence of prolonged droughts interceded by shorter periods of intense precipitation. If so, effective plague mitigation will become even more important.

Lessons beyond black-footed ferrets

The rich and dramatic history of black-footed ferrets provides lessons that may be applicable to conservation of other species at risk. Many of these lessons are clear, in hindsight, and are not a critique of past biologists, who often understood the problems but struggled with the hurdles of politics, sociology, and economics.

The primary lesson is that every effort should be made to preserve, or restore as quickly as possible, a species in the wild so that captive breeding and reintroduction are unnecessary. From the perspective of black-footed ferret program recovery coordinators, Lockhart et al. (2006, p.7) opined “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.” The costs of captive breeding and reintroduction of black-footed ferrets are difficult to calculate but easily exceeds several million dollars annually. The historic preservation of several wild black-footed ferret populations, particularly in the eastern part of the range where plague was not yet present (Figure 1.2), may have avoided the need for captive breeding and reintroduction efforts.

While preservation efforts should be made to negate the need for captive breeding, conservationists should also prepare for the possibility of captive breeding while wild populations are still relatively robust. Often the intricacies of a species’ breeding biology are unknown, particularly for species that are rare or difficult to observe. Also, by the time captive breeding is necessary for a species, there may not be excess animals available for learning objectives. While wild populations can still sustain the removal of some individuals, conservation partners could begin to experiment with captive breeding techniques to reduce uncertainties if captive breeding should be needed. Further, high-quality and diverse genetic samples should be preserved that could facilitate potential extreme measures such as cloning to increase genetic diversity. Captive breeding efforts with the Meeteetse black-footed ferrets in the 1980s benefited from lessons learned during the "failed" attempts with the Mellette County ferrets in the 1970s (Lockhart et al. 2006). Also, high quality tissue samples of at least two Meeteetse black-footed ferrets were cryopreserved, providing a basis for genetic rescue cloning today. But what if captive breeding with Meeteetse black-footed ferrets had been initiated earlier, as some biologists had suggested (Bogan 1985)? What if more black-footed ferrets had been rescued from Meeteetse? Or what if high quality tissue samples from the Mellette County black-footed ferrets had been preserved? The answer to all these questions is likely that black-footed ferret conservation would have benefited. We ask these questions to be instructive thought exercises for future biologists and managers that could help decision-making for other species.

Politics, sociology, and economics play significant and dynamic roles in the conservation of many species around the world, making the opportunities for significant conservation gain sometimes elusive or fleeting. Decisions that support conservation can often be made or overturned with a new political administration, social movement, or re-allocation of funding. Thus, conservationists should be prepared to take advantage of opportunities when they arise, even if they are not necessarily optimal.

Finally, the success of conservation efforts including recovery of black-footed ferrets will rely upon diverse partnerships and the creative ideas and problem solving that can emerge from such groups that agree to and are dedicated to a common cause. Black-footed ferret conservation efforts in the 1980s were often "marred by poor planning, inadequate resources, conflict, controversy, and crisis" (Lockhart et al. 2006, p. 9). This dynamic created tremendous in-fighting and likely delayed important decisions like removing individuals from the wild for captive breeding. In 1996, when the USFWS reassumed authority of the program, BFFRIT was established to include states, federal agencies, tribes, non-governmental organizations, zoos, and universities to advise and implement the recovery program. While politics cannot be eliminated, the strength of BFFRIT lies in multiple committees working with captive breeding, reintroduction, disease, and education/outreach. The USFWS and black-footed ferret recovery program is completely reliant upon these partnerships as demonstrated by the number of captive breeding facilities (one of six) and reintroduction sites (two of 28; Table 1.1) that are operated by the USFWS.

Conclusions

Black-footed ferret conservation and recovery has been partially successful in that the species was rescued from the brink of extinction, captive breeding efforts annually produce ~150 ferrets for reintroduction, and a handful of populations persist in the wild. The program still faces many difficult challenges, including genetic diversity and disease, although tools to mitigate these biological problems are being developed and implemented. A continuing and formidable challenge is improving the politics, collaboration, partnerships, sociology, and economics of prairie dog conservation. Changes in public lands prairie dog management policy are needed to allow the re-building, enhancement, and protection of large prairie dog colonies that function as ecosystems. It will involve continued engagement with landowners and agricultural interests to find solutions that work for all involved parties, but most importantly that provides enough habitat for self-sustaining, viable populations of black-footed ferrets. Funding these efforts of prairie dog protection, including plague management, will largely be borne by taxpayers. In this way, black-footed ferrets will be a species that is perpetually managed at some level, even after recovery goals are achieved. These are not easy tasks and the black-footed ferret recovery program clearly understands the issues. But "what we know about saving species is much greater than what we do about saving species" (Clark 1997). We know what needs to be done to restore black-footed ferrets to the North American prairies and we must redouble our efforts to do it.

Contributors

Co-authors on the publication produced from this chapter include Steven C. Forrest, Marc R. Matchett, and Stewart W. Breck. The authors would like to thank David Eads, Dean Biggins, John Hughes, and Mike Goldstein for critical reviews and suggestions.

Table 1.1: Black-footed ferret reintroduction sites, corresponding with Figure 1.2, including site characteristics and history.

Site (number corresponds to map Figure 1.2)	State or province	Year initiated	Ownership	Prairie dog species[1]	Potential or maximum size of prairie dog area[2]	Total # of release years	Total # black-footed ferrets released	Estimated # black-footed ferrets in fall 2019[3]	Highest annual estimated # of black-footed ferrets (year)[4]
Shirley Basin (1)	WY	1991	Federal, state, private	WTPD	X-Large	11	562	39	229 (2006)
UL Bend National Wildlife Refuge (2)	MT	1994	Federal	BTPD	Small	10	273	0	63 (2000)
Conata Basin/Badlands National Park (3)	SD	1994	Federal	BTPD	Large	12	382	120	355 (2007)
Aubrey Valley (4)	AZ	1996	Private, state	GPD	X-Large	17	546	20	123 (2012)
Fort Belknap Reservation (5)	MT	1997	Tribal	BTPD	Medium	7	247	15	55 (1998)
Coyote Basin (6)	UT	1999	Federal	WTPD	Large	16	517	1	45 (2003)
Cheyenne River Reservation (7)	SD	1999	Tribal	BTPD	Large	9	385	0	173 (2006)
Wolf Creek (8)	CO	2001	Federal	WTPD	Large	8	254	0	38 (2001)
BLM 40-complex (9)	MT	2001	Federal	BTPD	Small	4	95	0	10 (2004)

Janos (10)	Chihuahua, Mexico	2000	Community, private	BTPD	Large	6	299	0	15 (2003)
Rosebud Reservation (11)	SD	2004	Tribal	BTPD	Large	5	166	0	30 (2004)
Lower Brule Reservation (12)	SD	2006	Tribal	BTPD	Medium	8	190	13	29 (2010)
Wind Cave National Park (13)	SD	2007	Federal	BTPD	Small	6	113	20	49 (2010)
Espee Ranch (14)	AZ	2007	Private	GPD	X-Large	3	97	0	22 (2008)
Butte Creek Ranch (15)	KS	2007	Private	BTPD	Medium	8	241	14	79 (2011)
Northern Cheyenne Reservation (16)	MT	2008	Tribal	BTPD	Medium	4	88	0	6 (2009)
Vermejo Park Ranch (17)	NM	2008	Private	BTPD	Medium	7	163	0	28 (2010)
Grasslands National Park (18)	Saskatchewan, Canada	2009	Federal	BTPD	Medium	4	75	0	17 (2010)
Vermejo Park Ranch (19)	NM	2012	Private	GPD	Small	3	59	0	5 (2013)
Walker Ranch (20)	CO	2013	Private	BTPD	Small	3	121	3	3 (2014)
Soapstone Prairie/Meadow Springs Ranch (21)	CO	2014	City	BTPD	Small	6	125	8	11 (2016)

North-South Holly (22)	CO	2014	Private	BTPD	Medium	4	100	0	2 (2015)
Liberty (23)	CO	2014	Private	BTPD	Small	3	60	0	2 (2015)
Rocky Mountain Arsenal National Wildlife Refuge (24)	CO	2015	Federal	BTPD	Small	3	55	50	79 (2018)
Crow Reservation (25)	MT	2015	Tribal	BTPD	Medium	4	86	4	22 (2017)
Meeteetse (26)	WY	2016	Private, federal, state	WTPD	Medium	3	81	5	26 (2018)
Bad River Ranch (27)	SD	2017	Private	BTPD	Small	1	19	0	8 (2017)
Moore Ranch (28)	NM	2018	Private	BTPD	Small	2	12	3	3 (2018)
Total						177	5,411	315	1,520

[1] Prairie dog species: BTPD = black-tailed prairie dog, WTPD = white-tailed prairie dog, GPD = Gunnison's prairie dog.

[2] Potential or maximum recorded size of prairie dog colony area: Small = <2,000 hectares, Medium = 2,000-10,000 hectares, Large = 10,000-50,000 hectares, X-Large = >50,000 hectares.

[3] Minimum number alive estimate based upon annual spotlighting surveys.

[4] Highest minimum number alive observed.

Data based partially on USFWS (2019).

Figure 1.1: A black-footed ferret on a prairie dog burrow mound in South Dakota. Photo by Travis Livieri.

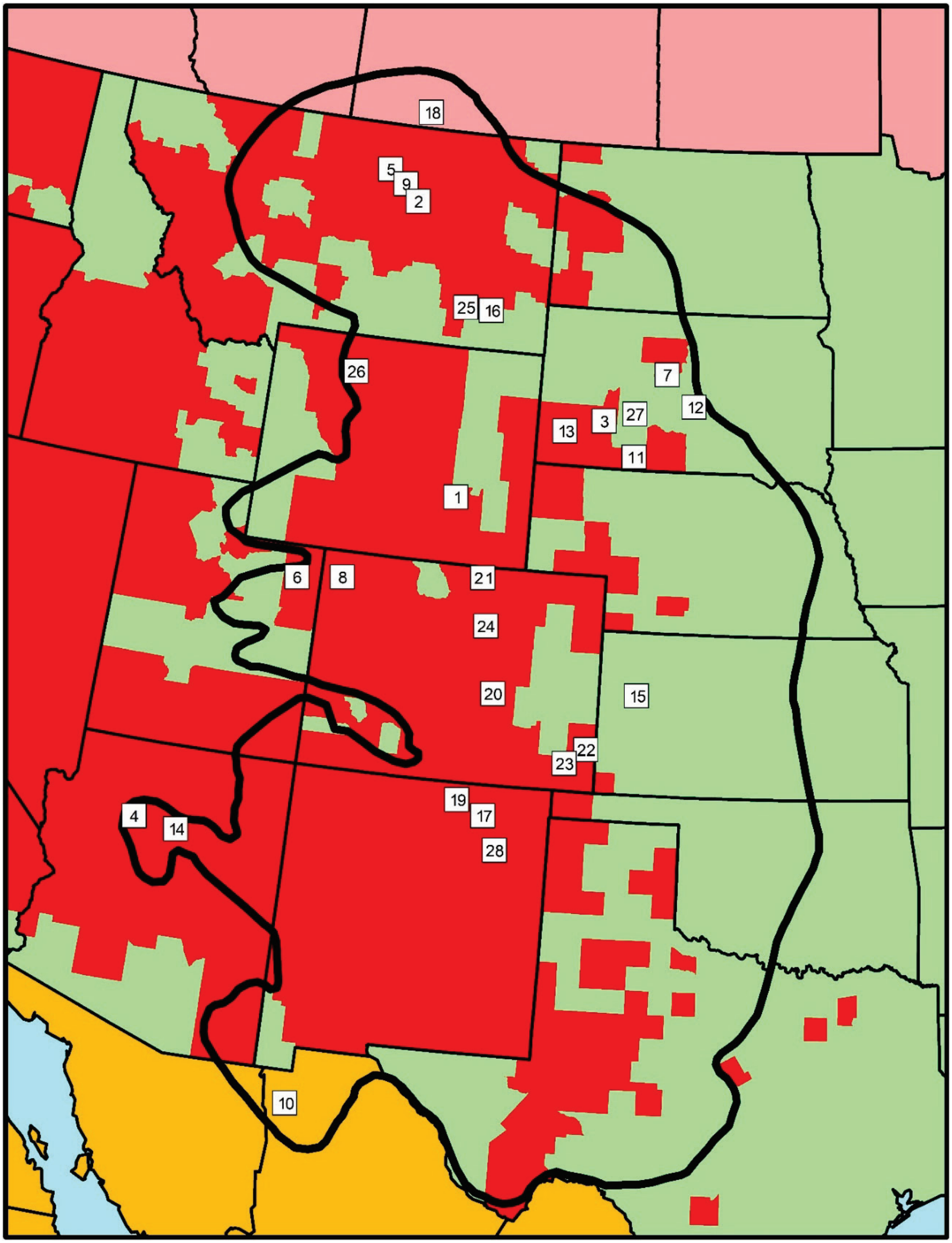

Figure 1.2: Historical range of black-footed ferrets (black outline) and reintroduction sites (numbered squares corresponding with Table 1.1). Counties in red have documented plague in animal or flea samples (partially based on Centers for Disease Control and Prevention data). Created by Travis Livieri.

Figure 1.3: Black-tailed prairie dogs on a burrow mound in Montana. Photo by Travis Livieri.

Figure 1.4: A black-tailed prairie dog colony in Grasslands National Park, Saskatchewan, Canada. Photo by Travis Livieri.

Figure 1.5: A black-footed ferret in a pre-release conditioning pen at the National Black-Footed Ferret Conservation Center, Carr, Colorado. Photo by Travis Livieri.

Figure 1.6: Black-footed ferret cages at the National Black-Footed Ferret Conservation Center, Carr, Colorado. Photo by Travis Livieri.

Figure 1.7: Black-footed ferret in a live-trap for vaccination against plague in South Dakota. Photo by Travis Livieri.

REFERENCES

Achtman, M., K. Zurth, G. Morelli, G. Torrea, A. Guiyoule, and E. Carniel. 1999. *Yersinia pestis*, the cause of plague, is a recently emerged clone of *Yersinia pseudotuberculosis*. Proceedings of the National Academy of Sciences 96:14043-14048. https://doi.org/10.1073/pnas.96.24.14043

Anderson, E., S. C. Forrest, T. W. Clark, and L. Richardson. 1986. Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851. Great Basin Naturalist Memoirs 8:11-62. https://scholarsarchive.byu.edu/gbnm/vol8/iss1/3

Antolin, M. F., P. Gober, B. Luce, D. E. Biggins, W. E. Van Pelt, D. B. Seery, M. Lockhart, and M. Ball. 2002. The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. Transactions of the 67th North American Wildlife and Natural Resources Conference 67:104-127. https://digitalcommons.unl.edu/usfwspubs/57/

Audubon, J. J., and J. Bachman. 1851. The viviparous quadrupeds of North America. V. G. Audubon, New York. Vol. 2. 334 pp

Biggins, D. E., and D. A. Eads. 2017. Evolution, natural history, and conservation of black-footed ferrets. Pages 340-356 in D. W. MacDonald, C. Newman, and L. A. Harrington, editors. Biology and Conservation of Musteloids. Oxford University Press.

Biggins, D. E., J. L. Godbey, K. L. Gage, L. G. Carter, and J. A. Montenieri. 2010. Vector control improves survival of prairie dogs (*Cynomys*) in areas considered enzootic for plague. Vector-Borne and Zoonotic Diseases 10:17-26. https://doi.org/10.1089/vbz.2009.0049

Biggins, D. E., J. L. Godbey, L. R. Hanebury, B. Luce, P. E. Marinari, M. R. Matchett, and A. Vargas. 1998. The effect of rearing methods on survival of reintroduced black-footed ferrets. Journal of Wildlife Management 62:643-653. https://doi.org/10.2307/3802340

Biggins, D. E., J. L. Godbey, B. M. Horton, and T. M. Livieri. 2011. Movements and survival of black-footed ferrets associated with an experimental translocation in South Dakota. Journal of Mammalogy 92:742-50. https://doi.org/10.1644/10-MAMM-S-152.1

Biggins, D. E., J. L. Godbey, M. R. Matchett and T. M. Livieri. 2006. Habitat preferences and intraspecific competition in black-footed ferrets. Pages 129-140 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://pubs.usgs.gov/publication/70180909

Biggins, D. E., and M. Y. Kosoy. 2001. Influences of introduced plague on North American mammals: implications from ecology of plague in Asia. Journal of Mammalogy 82:906-916. https://doi.org/10.1644/1545-1542(2001)082<0906:IOIPON>2.0.CO;2

Biggins, D. E., A. Vargas, J. L. Godbey, and S. H. Anderson. 1999. Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*). Biological Conservation 89:121-129. https://doi.org/10.1016/S0006-3207(98)00158-X

Bogan, M. A. 1985. Needs and direction for future black-footed ferret research. Pages 28.1-28.5 in S. H. Anderson and D. B. Inkley, editors. Black-footed ferret workshop proceedings. Wyoming Game and Fish Department, Cheyenne, Wyoming.

Brickner, K. M., M. B. Grenier, A. E. Crosier, and J. N. Pauli. 2014. Foraging plasticity in a highly specialized carnivore, the endangered black-footed ferret. Biological Conservation 169:1-5. https://doi.org/10.1016/j.biocon.2013.10.010

Cahalane, V. H. 1954. Status of the black-footed ferret. Journal of Mammalogy 35:418-424. https://doi.org/10.2307/1375967

Campbell III, T. M., T. W. Clark, L. Richardson, S. C. Forrest, and B. R. Houston. 1987. Food habits of Wyoming black-footed ferrets. American Midland Naturalist 117:208-210. https://doi.org/10.2307/2425722

Carpenter, J. W., M. J. G. Appel, R. C. Erickson, and M. N. Novilla. 1976. Fatal vaccine-induced canine distemper virus in black-footed ferrets. Journal of the American Veterinary Medical Association 169:961-964. https://europepmc.org/article/med/988011

Carpenter, J. W., J. P. Davidson, M. N. Novilla, and J. C. M. Huang. 1980. Metastatic, papillary cystadenocarcinoma of the mammary gland in a black-footed ferret. Journal of Wildlife Diseases 16:587-592. https://doi.org/10.7589/0090-3558-16.4.587

Clark, T. W. 1987. Black-footed ferret recovery: a progress report. Conservation Biology 1:8-11. https://www.jstor.org/stable/2386120

Clark, T. W. 1989. Conservation biology of the black-footed ferret. Wildlife Preservation Trust Special Scientific Report 3. Wildlife Preservation Trust International, Philadelphia, Pennsylvania.

Clark, T. W. 1997. Averting extinction: reconstructing endangered species recovery. Yale University Press, New Haven, Connecticut.

Coues, E. 1877. Fur-bearing animals: a monograph of North American Mustelidae. Department of Interior USGS Miscellaneous Publication.

Eads, D. A., and D. E. Biggins. 2015. Plague bacterium as a transformer species in prairie dogs and the grasslands of western North America. Conservation Biology 29:1086-1093. https://doi.org/10.1111/cobi.12498

Eads, D. A., and D. E. Biggins. 2017. Paltry past-precipitation: Predisposing prairie dogs to plague? Journal of Wildlife Management 81:990-998. https://doi.org/10.1002/jwmg.21281

Eads, D. A., and D. E. Biggins. 2019. Plague management of prairie dog colonies: degree and duration of deltamethrin flea control. Journal of Vector Ecology 44:40-47. https://doi.org/10.1111/jvec.12327

Eads, D. A., D. E. Biggins, J. Bowser, K. Broerman, T. M. Livieri, E. Childers, P. Dobesh, and R. L. Griebel. 2019. Evaluation of five pulicides to suppress fleas on black-tailed prairie dogs: encouraging long-term results with systemic 0.005% fipronil. Vector-Borne and Zoonotic Diseases 19:400-406. https://doi.org/10.1089/vbz.2018.2339

Eads, D. A., D. E. Biggins, J. Bowser, J. C. McAllister, R. L. Griebel, E. Childers, T. M. Livieri, C. Painter, L. Sterling Krank, and K. Bly. 2018. Resistance to deltamethrin in prairie dog (*Cynomys ludovicianus*) fleas in the field and in the laboratory. Journal of Wildlife Diseases 54:745-754. https://doi.org/10.7589/2017-10-250

Eads, D. A., D. E. Biggins, D. S. Jachowski, T. M. Livieri, J. J. Millspaugh, and M. Forsberg. 2010. Morning ambush attacks by black-footed ferrets on emerging prairie dogs. Ethology Ecology & Evolution 22:345-352. https://doi.org/10.1080/03949370.2010.510037

Eads, D. A., and D. Marsh. 2020. Possible litter of seven wild black-footed ferret kits. Western North American Naturalist 80:543-546. https://doi.org/10.3398/064.080.0413

Eads, D.A., J. J. Millspaugh, D. E. Biggins, T. M. Livieri, and D. S. Jachowski. 2011. Postbreeding resource selection by adult black-footed ferrets in the Conata Basin, South Dakota. Journal of Mammalogy 92:760-770. https://doi.org/10.1644/10-MAMM-S-139.1

Eads, D. A., D. E. Biggins, T. M. Livieri, and J. J. Millspaugh. 2014. Space use, resource selection and territoriality of black-footed ferrets: implications for reserve design. Wildlife Biology 20:27-36. https://doi.org/10.2981/wlb.13070

Forrest, S. C., D. E. Biggins, L. Richardson, T. W. Clark, T. M. Campbell III, K. A. Fagerstone, and E. T. Thorne. 1988. Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981-1985. Journal of Mammalogy 69:261-273. https://doi.org/10.2307/1381377

Forrest, S. C., and J. C. Luchsinger. 2006. Past and current chemical control of prairie dogs. Pages 115-128 in J. L. Hoogland, editor. Conservation of the black-tailed prairie dog: saving North America's western grasslands. Island Press, Washington, D. C.

Fox, N. S., S. C. Wallace, and J. I. Mead. 2017. Fossil *Mustela nigripes* from Snake Creek Burial Cave, Nevada, and implications for black-footed ferret paleoecology. Western North American Naturalist 77:137-151. https://doi.org/10.3398/064.077.0202

Garst, W. E. 1954. Black-footed ferret in South Dakota. Journal of Mammalogy 35:594. https://doi.org/10.2307/1375599

Godbey, J. L., D. E. Biggins, and D. Garelle. 2006. Exposure of captive black-footed ferrets to plague and implications for species recovery. Pages 233-237 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://doi.org/10.3133/sir20055293

Grenier, M. B., D. B. McDonald, and S. W. Buskirk. 2007. Rapid population growth of a critically endangered carnivore. Science 317:779. https://doi.org/10.1126/science.1144648

Hanebury, L. R, and D. E. Biggins. 2006. A history of searches for black-footed ferrets. Pages 47-65 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://pubs.usgs.gov/publication/70180906

Henderson, F. R., P. F. Springer, and R. Adrian. 1969. The black-footed ferret in South Dakota. South Dakota Game, Fish and Parks Technical Bulletin No. 4. Pierre, South Dakota.

Hillman, C. N. 1968. Life history and ecology of the black-footed ferret in the wild. MS Thesis, South Dakota State University. Brookings, South Dakota. https://openprairie.sdstate.edu/etd/133

Hillman, C. N., and J. W. Carpenter. 1984. Breeding biology and behaviour of captive black-footed ferrets *Mustela nigripes*. International Zoo Yearbook 23:186-191. https://doi.org/10.1111/j.1748-1090.1984.tb03030.x

Jachowski, D. S., and J. M. Lockhart. 2009. Reintroducing the black-footed ferret *Mustela nigripes* to the Great Plains of North America. Small Carnivore Conservation. 41:58-64. https://smallcarnivoreconservation.com/index.php/sccg/issue/view/280/82

Koepfli, K. P., K. A. Deere, G. J. Slater, C. Begg, K. Begg, L. Grassman, M. Lucherini, G. Veron, and R. K. 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biology 6:10 https://doi.org/10.1186/1741-7007-6-10

Lantz, D. E. 1903. Destroying prairie dogs and pocket gophers. Kansas Agricultural

Experimental Station, Manhattan, Bulletin 116:147-163.

Livieri, T. M., and E. M. Anderson. 2012. Black-footed ferret home ranges in Conata Basin, South Dakota. Western North American Naturalist 72:196-205. https://doi.org/10.3398/064.072.0209

Livieri, T. M., D. S. Licht, B. J. Moynahan, and P. D. McMillan. 2013. Prairie dog aboveground aggressive behavior towards black-footed ferrets. American Midland Naturalist 169:422-425. https://doi.org/10.1674/0003-0031-169.2.422

Lockhart, J. M., E. T. Thorne, and D. R. Gober. 2006. A historical perspective on recovery of the black-footed ferret and the biological and political challenges affecting its future. Pages 6-19 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://doi.org/10.3133/sir20055293

Marinari, P. E., and J. S. Kreeger. 2006. An adaptive management approach for black-footed ferrets in captivity. Pages 23-36 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://doi.org/10.3133/sir20055293

Matchett, M. R., D. E. Biggins, V. Carlson, B. Powell and T. Rocke. 2010. Enzootic plague reduces black-footed ferret (*Mustela nigripes*) survival in Montana. Vector-Borne and Zoonotic Diseases 10:27-35. https://doi.org/10.1089/vbz.2009.0053

Matchett, M. R., D. A. Eads, J. Cordova, T. M. Livieri, H. Hicks, and D. E. Biggins. 2023. Flea control on prairie dogs (*Cynomys* spp.) with fipronil bait pellets: potential plague mitigation tool for rapid field application and wildlife conservation. Journal of Wildlife Diseases 59:71-83. https://doi.org/10.7589/JWD-D-22-00008

Miller, B., and R. P. Reading. 2012. Challenges to black-footed ferret recovery: protecting prairie dogs. Western North American Naturalist 72:228-240. https://doi.org/10.3398/064.072.0212

Miller, B. J., R. P. Reading, D. E. Biggins, J. K. Detling, S. C. Forrest, J. L. Hoogland, J. Javersak, S. D. Miller, J. Proctor, J. Truett, and D. W. Uresk. 2007. Prairie dogs: an ecological review and current biopolitics. The Journal of Wildlife Management 71:2801-2810. https://doi.org/10.2193/2007-041

Novak, B. J., T. Maloney, and R. Phelan. 2018. Advancing a new toolkit for conservation: from science to policy. The CRISPR Journal 1:11-15. https://doi.org/10.1089/crispr.2017.0019

Owen, P. R., C. J. Bell, and E. M. Mead. 2000. Fossils, diet, and conservation of black-footed ferrets (*Mustela nigripes*). Journal of Mammalogy 81:422-433. https://doi.org/10.1644/1545-1542(2000)081<0422:FDACOB>2.0.CO;2

Powell, R.A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. Zeitschrift für Tierpsychologie 50:153-165. https://doi.org/10.1111/j.1439-0310.1979.tb01023.x

Rocke, T. E., S. Smith, P. Marinari, J. Kreeger, J. T. Enama, and B. S. Powell. 2008. Vaccination with F1-V fusion protein protects black-footed ferrets (*Mustela nigripes*) against plague upon oral challenge with *Yersinia pestis*. Journal of Wildlife Diseases 44:1-7. https://doi.org/10.7589/0090-3558-44.1.1

Rocke, T. E., D. W. Tripp, R. E. Russell, R. C. Abbott, K. L. D. Richgels, M. R. Matchett, D. E.

Biggins, R. Griebel, G. Schroeder, S. M. Grassel, D. R. Pipkin, J. Cordova, A. Kavalunas, B. Maxfield, J. Boulerice, and M. W. Miller. 2017. Sylvatic plague vaccine partially protects prairie dogs (*Cynomys* spp.) in field trials. Ecohealth 14:438-450. https://doi.org/10.1007/s10393-017-1253-x

Santymire, R. M., E. V. Lonsdorf, C. M. Lynch, D. E. Wildt, P. E. Marinari, J. S. Kreeger, and J. G. Howard. 2019. Inbreeding causes decreased seminal quality affecting pregnancy and litter size in the endangered black-footed ferret. Animal Conservation 22:331-340. https://doi.org/10.1111/acv.12466

Sheets, R. G., R. L. Linder, and R. B. Dahlgren. 1972. Food habits of two litters of black-footed ferrets in South Dakota. American Midland Naturalist 87:249-251. https://doi.org/10.2307/2423900

Tretten, T. N. 2019. Rarely observed behaviors and occurrences of black-footed ferrets preconditioning for wild release 2014–2017. Journal of Fish and Wildlife Management 10:241-249. https://doi.org/10.3996/042018-JFWM-030

U. S. Fish and Wildlife Service. 2013. Recovery plan for the black-footed ferret (*Mustela nigripes*). Department of the Interior, Washington, D.C. https://www.fws.gov/node/68191

U. S. Fish and Wildlife Service. 2019. Species status assessment report for the black-footed ferret (*Mustela nigripes*). Carr, Colorado. https://ecos.fws.gov/ServCat/DownloadFile/169265

Williams, E. S., E. T. Thorne, T. J. Quan, and S. L. Anderson. 1991. Experimental infection of domestic ferrets (*Mustela putorius furo*) and Siberian polecats (*Mustela eversmanni*) with *Yersinia pestis*. Journal of Wildlife Diseases 27:441-445. https://doi.org/10.7589/0090-3558-27.3.441

Williams, E. S., K. Mills, D. R. Kwiatkowski, E. T. Thorne, and A. Boerger-Fields. 1994. Plague in a black-footed ferret (*Mustela nigripes*). Journal of Wildlife Diseases 30:581-585. https://doi.org/10.7589/0090-3558-30.4.581

Wisely, S. M., O. A. Ryder, R. M. Santymire, J. F. Engelhardt, and B. L. Novak. 2015. A road map for 21st century genetic restoration: gene pool enrichment of the black-footed ferret. Journal of Heredity 106:581-592. https://doi.org/10.1093/jhered/esv041

Wisely, S. M., R. M. Santymire, T. M. Livieri, S. A. Mueting, and J. G. Howard. 2008. Genotypic and phenotypic consequences of reintroduction history in the black-footed ferret (*Mustela nigripes*). Conservation Genetics 9:389-399. https://doi.org/10.1007/s10592-007-9351-x

2. MANAGING MULTIPLE IMPACTS OF A DISEASE IN AN ENDANGERED CARNIVORE: BLACK-FOOTED FERRETS, PRAIRIE DOGS, AND PLAGUE

Summary

Diseases can directly and indirectly impact wildlife populations, but understanding these effects in endangered species is challenging because rare species typically have small populations and comparative data before and after disease events may not exist. Ideally, effective disease monitoring strategies in susceptible wildlife populations would inform timely mitigation if diseases emerge. Plague, a bacterial disease invasive to North America and caused by *Yersinia pestis*, causes high mortality in endangered black-footed ferrets (*Mustela nigripes*) and their prairie dog prey (*Cynomys* spp.). We evaluated plague surveillance and the impacts of mitigation efforts on annual survival of black-footed ferrets and the persistence of prairie dog colonies in South Dakota. To detect a plague epizootic, we sampled serology of 812 carnivores and tested 111 prairie dogs. To mitigate impacts of plague we annually dusted prairie dog burrows ($\bar{x}$ = 418,226, SE = 49,798) with insecticides for flea vector control and vaccinated 847 black-footed ferrets. Dusting maintained the area of prairie dog colonies that had signs of prairie dog activity while non-dusted colonies decreased in active area by 96.6%. Estimated black-footed ferret annual survival increased 49-78% on dusted colonies, and vaccination increased ferret survival an additional 13-20%. Our results suggest that epizootic plague may be detected in time for effective mitigation and the combined efforts of vector control and vaccination of black-footed ferrets can be highly effective for recovery of this endangered species.

Introduction

Endangered species face a wide variety of threats, including habitat loss, invasive species, pollution, overexploitation and disease, factors that often work synergistically to push species towards extinction (Heard et al. 2013, Ducatez and Shine 2017, Hu et al. in press). Although disease is rarely identified as the primary cause of endangerment (Smith et al. 2006), emerging or re-emerging infectious diseases have recently increased in frequency to pose threats to many wildlife species (Daszak et al. 2000, Jones et al. 2008, Tompkins et al. 2015). Common and abundant species may ultimately survive catastrophic epizootics, but small endangered populations could suffer irreversible declines (McCallum and Dobson 1995, Woodroffe 1999, Breed et al. 2009, Smith et al. 2009, Russell et al. 2020).

Disease effects on endangered species are often direct, causing mortality, reducing populations and/or modifying behaviors (Preece et al. 2017). Vulnerable species may be impacted by multiple diseases. For instance, island foxes (*Urocyon littoralis*) on the California Channel Islands were exposed to four diseases that may have contributed to their decline (Clifford et al. 2006), and the smallest extant population of Ethiopian wolves (*Canis simensis*) was drastically reduced by rabies and canine distemper (Marino et al. 2017). Alternatively, diseases that impact an abundant or keystone species may have indirect, cascading effects upon a reliant endangered species (de Castro and Bolker 2005, Collinge et al. 2008) or ecosystem (Selakovic et al. 2014). For example, rabbit hemorrhagic disease virus caused declines in European rabbits (*Oryctolagus cuniculus*), a key prey item, leading to decreases in two endangered predators, the Iberian lynx (*Lynx pardinus*) and the Spanish imperial eagle (*Aquila adalberti;* Monterroso et al. 2016).

Understanding the effects of disease on endangered populations is hindered by the difficulty of separating disease impacts from other factors that led to endangerment (Scott 1988, McCallum and Dobson 1995), the scarcity of population data from before and after disease detection (McCallum and Dobson 1995, Tompkins et al. 2015), and the inherent challenge of studying rare species, especially those that are difficult to detect (Chades et al. 2011, Preece et al. 2017). Carcasses may be difficult to locate for rare species, such that disease epizootics are usually detected well after they have begun (McCallum and Dobson 1995). Ideally, a disease monitoring strategy would include population surveillance prior to the emergence of disease and subsequent study of the disease incidence and morbidity/mortality caused by the disease so that effective management and mitigation strategies can be implemented (Artois et al. 2009, Grogan et al. 2014).

Strategies to manage and mitigate disease in wild populations include targeting the pathogen and vectors directly, manipulating the hosts, or changing the environment (Wisely 2019). Removal of infected individuals from the population was a successful strategy for Tasmanian devils (*Sarcophilus harrisi)* with devil facial tumor disease, resulting in a reduction of large tumors and maintenance of high animal densities compared to an area without removals (Jones et al. 2007). Vaccination can be an effective strategy for conserving populations of endangered species, such as Ethiopian wolves (Haydon et al. 2006) and Iberian lynx (Lopez et al. 2009). However, the efficacy of vaccination can be difficult to evaluate in endangered species because low sample sizes and concern over putting the species at further risk often preclude the use of a non-vaccinated control group (Woodroffe 1999, Breed et al. 2009, Cleaveland 2009). Despite these examples of successful disease intervention to conserve endangered species and a recognized need for rigorous evaluations of mitigation, many disease management programs rely on epidemiological models or frameworks that have yet to be fully implemented and evaluated (Woodroffe 1999, Delahay et al. 2009, Scheele et al. 2014). Here we present a case study and evaluation of a multi-faceted effort to manage multiple impacts of sylvatic plague (plague hereafter), caused by the introduced bacterium *Yersinia pestis*, in a free-ranging population of endangered black-footed ferrets (*Mustela nigripes*), in Conata Basin, a portion of the Buffalo Gap National Grasslands, and the adjacent Badlands National Park (CB/BADL), in southwestern South Dakota. The black-footed ferret population at CB/BADL is the largest reintroduced free-ranging population of the species studied to date (Livieri et al. 2022).

The endangered black-footed ferret is an obligate predator of prairie dogs (*Cynomys* spp.) and uses prairie dog colonies and burrows as habitat (Biggins et al. 2006c). Both animals are highly susceptible to plague. Prairie dogs are hosts of plague, exhibiting low resistance and high mortality, and their plague risk is exacerbated by their typically heavy infestations of flea vectors (Gage and Kosoy 2006). Black-footed ferrets are incidental hosts of *Y. pestis*, suffering multiple impacts, including direct mortality, loss of prey (prairie dogs), and loss of habitat (prairie dog colonies and burrows; Eads and Biggins 2015). Conversion of native prairie habitat, extensive prairie dog poisoning campaigns, and disease caused widespread decline and extirpation of black-footed ferrets from most parts of their historic range by the 1970’s with only two remnant populations studied: one in Mellette County, South Dakota from 1964-1974, and one near Meeteetse, Wyoming from 1981-1987 (Forrest et al. 1988, U. S. Fish and Wildlife Service 2013). The last remaining individuals of the species were removed from the wild by 1987 to establish a captive breeding program and reintroductions back into the wild, which began in 1991. Reintroductions have occurred throughout the historic range of black-footed ferrets in eight U.S. States and portions of Mexico and Canada with varying degrees of success (Jachowski and Lockhart 2009, U. S. Fish and Wildlife Service 2013, Livieri et al. 2022).

Managing disease for black-footed ferrets, both in captivity and the wild, has been a high priority for the recovery program (Marinari and Kreeger 2006, U. S. Fish and Wildlife Service 2013). Historically, the primary concern regarding disease in black-footed ferrets was focused on canine distemper virus rather than plague, because ten black-footed ferrets from Mellette County (four in 1971) and six from Meeteetse (1985) died of canine distemper in captivity (Carpenter et al. 1976, Williams et al. 1988). Further, black-footed ferrets were mistakenly assumed to be resistant to plague (Williams et al. 1991, 1994). More recently, 27 of 30 captive black-footed ferrets died after being accidentally fed plague-infected prairie dogs, demonstrating the high lethality of plague for black-footed ferrets (Godbey et al. 2006). Field studies confirmed the insidious and often undetectable effects of plague on prairie dogs (Biggins et al. 2010) and black-footed ferrets (Matchett et al. 2010). Both plague and canine distemper are highly fatal to black-footed ferrets, but plague has likely played a historically underestimated and important role in the near extinction of the species.

Plague is a vector-borne disease that was accidentally introduced to North America around 1900 and quickly spread eastward across the western half of the United States, causing fatalities in many wildlife species, primarily rodents (Biggins and Kosoy 2001, Antolin et al. 2002). By the 1930's the disease had spread to the ranges of white-tailed (*C. leucurus*) and Gunnison's (*C. gunnisoni*) prairie dogs (Eskey and Haas 1940) and eventually further eastward into the range of black-tailed prairie dogs (*C. ludovivianus*). As prairie dog populations were impacted and became increasingly fragmented, the black-footed ferret was pushed to the brink of extinction. Plague spread to eastern Wyoming by the 1940's but was not detected east of the

Black Hills in South Dakota until 2005 (Mize and Britten 2016). Plague was detected in 2008 in the CB/BADL area, prompting project managers and partners to undertake extensive efforts to protect the black-footed ferret and prairie dog populations. Here, we describe a long-term field study documenting the first known invasion of plague into CB/BADL and its effects on prairie dog colonies and reintroduced black-footed ferret populations. We used carnivore serology, diurnal searches for prairie dog carcasses, and observations of prairie dog activity to document the prevalence of plague and canine distemper in the study area. We also evaluated the effects of disease management, flea vector control, and direct vaccination of black-footed ferrets on prairie dog colony (i.e., ferret habitat) size and ferret survival. We demonstrate how managing the multiple impacts of a single disease appears to have prevented extirpation of this important black-footed ferret population.

Methods

Disease surveillance

Surveillance occurred annually for plague (1990-2009) and canine distemper (1990-2006) using carnivore seroprevalence (Gage et al. 1994, Schuler et al. 2021) and veterinary diagnostic tests to inform black-footed ferret recovery actions at CB/BADL. Between 1990 and 2009 we harvested, live-trapped with release, or opportunistically sampled 560 coyotes (*Canis latrans*), 114 American badgers (*Taxidea taxus*), 23 raccoons (*Procyon lotor*), 44 striped skunks (*Mephitis mephitis*), three bobcats (*Lynx rufus*), 61 swift fox (*Vulpes velox*), and seven red fox (*Vulpes vulpes*) for serological testing. We sent carcasses, sera, and blood samples on filter paper to Wyoming State Veterinary Laboratory (Laramie, WY; WYSVL) or United States Department of Agriculture National Wildlife Research Center (Fort Collins, CO) for testing. Carcasses of black-tailed prairie dogs (n = 111) found dead in the field or that died during quarantine as food for captive black-footed ferrets were sent to WYSVL or Centers for Disease Control (Fort Collins, CO) for plague testing by direct fluorescent antibody or bacterial culture (Gage 1999). In 2007 we ceased seroprevalence surveillance efforts for canine distemper because our results suggested the disease was common in the area. Similarly, we ceased active carnivore seroprevalence surveillance for plague in 2010 after the confirmed invasion of plague in 2008, although other research in the area documented the continued presence of plague in carnivores through 2016 (Mize 2015, Nevison 2017). We calculated annual prevalence for both canine distemper and plague as the proportion of individuals sampled that were detected with disease or serological evidence of exposure (Thrusfield and Christley 2018) bracketed by 95% binomial exact confidence intervals.

Diurnal ground surveys of prairie dog activity on colonies were conducted to infer the presence of plague in addition to serological and diagnostic tests. Plague epizootics are the only known disease events that can cause large-scale mortality in black-tailed prairie dogs (Barnes 1993, Biggins et al. 2021). Plague presence was suspected if few or no prairie dogs were observed on a colony after several visits on consecutive days and vegetation was emerging on or near burrow mounds. We mapped the extent of the inactive area with a Trimble Global Positioning Systems (GPS) unit, and these data were imported into ArcGIS 9.1. We conducted weekly or monthly ground surveys in the summer months beginning in 2005 and continuing through 2015, and other field activities (e.g., black-footed ferret surveys, prairie dog colony mapping, insecticide dust application) also contributed to assessing prairie dog activity that may have indicated the presence of plague.

Disease management

We controlled fleas, the vector of plague, through application of a pulicide dust (DeltaDust, Bayer Environmental Science, Research Triangle Park, NC; active ingredient 0.05% delatmethrin) into prairie dog burrows (Biggins et al. 2010, Matchett et al. 2010). We applied dust once per year during spring-fall at a rate of ~6 g per burrow opening (Table 2.1) to $\bar{x}$ = 418,226 (SE = 49,798) burrows on $\bar{x}$ = 3,374 (SE =418) ha of prairie dog colonies (Table 2.1, Figure 2.1). In 2005, when plague was detected in a prairie dog complex ~48km to the south, we prophylactically dusted a subset of colonies at CB/BADL. Dusting was initiated in 2005 on 8 prairie dog colonies (2,838.1 ha), continued on 2 colonies in 2006-2007, then expanded to additional colonies with the confirmed invasion of plague in 2008. After 2008, we re-dusted colonies annually through 2016. As more funding became available after 2008, 41 additional prairie dog colonies were dusted (Table 2.1, Appendix Figures S1-S13). We selected prairie dog colonies for dusting based upon black-footed ferret presence and density, with the goal of maximizing preservation of ferrets by dusting as many ferret-occupied prairie dog colonies as possible.

We vaccinated 847 black-footed ferrets during nocturnal spotlight surveys, which were used to locate and count ferrets on prairie dog colonies from August-November 1998-2017 and occasionally at other times of the year (Biggins et al. 2006a). We captured animals in live-traps, anesthetized them with isoflurane at a mobile station, implanted a passive integrated transponder (PIT) tag (AVID Friendchip 125 kHz, Norco, CA) for individual identification (Black-Footed Ferret Recovery Implementation Team 2016), and injected one dose of F1-V fusion protein plague vaccine (Rocke et al. 2008, Matchett et al. 2010). We administered a second dose of F1-V to black-footed ferrets upon recapture, even if recapture occurred in a subsequent year. After processing, we immediately returned all animals to the point of capture. Our goal was to vaccinate all black-footed ferrets with a total of two doses of vaccine, with at least one month between doses, which should confer lifetime protection against plague (Rocke et al. 2008). Not all ferrets received two doses because they were not all recaptured, and occasional temporary vaccine shortages left some ferrets without vaccine. All black-footed ferret activities were conducted under United States Fish and Wildlife Service Endangered Species permit #TE064682-1 and followed the animal handling guidelines of Sikes and the Animal Care and Use Committee of the American Society of Mammalogists (2016).

Evaluation of disease management

We evaluated the effects of disease management (dusting and vaccination) on prairie dog colony size and black-footed ferret survival. We mapped all prairie dog colonies in CB/BADL biennially from 2007-2017 with GPS by circumscribing the outer-most prairie dog burrows (Biggins et al. 2006d) and imported data into Geographic Information Systems (GIS) to calculate colony area. Using the 2007 prairie dog colony GIS layer, which was the year of the largest colony extent, we assigned each polygon a unique identifier and used that same identifier if the polygon fragmented in subsequent years. Colony polygons that were partially dusted were split in the GIS layer to track the size of dusted and non-dusted areas. We compared the change in total colony area (hectares) of all dusted and non-dusted prairie dog colonies at 2-year intervals to evaluate the effects of dusting on black-footed ferret habitat. If a colony was dusted once in a 2-year interval, then we categorized it as dusted for that interval.

We estimated annual survival of 1,774 wild-born black-footed ferrets from 1998-2017 (Table 2.2), excluding all animals that were translocated out of the population and all captive-born black-footed ferrets released into CB/BADL because pre-release conditioning affects survival rates (Biggins et al. 1998). We used the Barker model (Barker et al. 2004) in Program MARK (White and Burnham 1999), a joint live-dead model that uses resightings outside of the primary recapture periods to increase precision of survival estimates (Sandercock 2006). It estimates survival from sampling period t to $t + 1$ (S_t), probability of capture in sampling period t (p_t), probability an animal that dies in the interval (t, $t + 1$) is found and reported (r_t), the probability an animal that survives the interval (t, $t + 1$) is resighted in the interval (R_t), the probability an animal that dies in the interval (t, $t + 1$) and is not reported and is instead resighted alive in that interval before dying (R_t'), site fidelity (F_t), and immigration (F_t '). We fixed r = 0 because direct observation of black-footed ferret mortality is rare and we directly observed only seven deaths over 20 years. We assumed $F = 1$, no emigration, because we had no sampling effort outside the study area with which to inform this parameter. Models included covariates for sex, colony dusting, plague vaccination (0, 1, 2 doses), and distance to known plague. We ranked models using Akaike's Information Criterion (AIC; Burnham and Anderson 2004) and considered models within 5 AIC units of the top model as informative.

The primary annual period for detecting black-footed ferrets by spotlighting surveys was 16 August – 8 November because we surveyed >75% of the study area every year between those dates. We conducted occasional spotlight surveys outside of the primary period, and these data were considered auxiliary, helping to refine estimates of both S and p. Black-footed ferrets entered the data set upon their first capture in a primary period as a juvenile or adult and were considered to be adults in their second primary period. Animals that were first captured during the auxiliary period were not included in the data set until they were resighted during a primary period and entered as adults. Beginning in 2005, each animal in the data set was coded for occupation of a dusted (1) or non-dusted (0) prairie dog colony in the same year. After the last detection of an animal, the dusting status of the last occupied colony was used for the remainder of the detection history. Each black-footed ferret was also coded for plague vaccination status that was cumulative up to two doses in the ferret's lifetime and carried through the detection history. Beginning with the 2007 primary period, we used GIS to annually measure distance to plague (km) for each black-footed ferret as the distance between the first capture point location of a primary period and the proximate polygon edge of current or past suspected plague presence as mapped during disease surveillance.

We annually (1 May – 30 April) estimated the black-footed ferret population at CB/BADL as the minimum number alive (MNA; Black-Footed Ferret Recovery Implementation Team 2016) identified by PIT tag and retrospectively revised estimates with PIT-tagged ferrets missed during the previous year and newly tagged adults (i.e., undetected but alive in the previous year). We used the number of PIT-tagged black-footed ferrets during the primary period (16 August – 8 November) divided by p_t, probability of capture in a sampling period, to estimate population size during the primary period which we compared to estimated survival rates to better understand the effects of plague, dusting, and vaccine (e.g., whether the population trended downward when plague was documented). We calculated % change in black-footed ferret survival within a period as $((S_{t,\text{no plague mangement}} - S_{t,\text{dusted}})/ S_{t,\text{no plague management}})*100$ to estimate the effect of dusting status and vaccination.

Results

Disease surveillance

Of the 812 carnivores we submitted for serological testing, we detected plague twice prior to 2008, in 1994 and 2005, both times in coyote sera (Table 2.3, Figure 2.2), but we did not observe any evidence of a plague epizootic, such as widespread decline in prairie dog activity. In 2008 plague titers were detected in serology of six individuals of two different species (three coyotes and three swift fox), and seven prairie dog carcasses tested positive using fluorescent antibody tests. We also observed colonies (burrows) without activity across 6,563.9 ha of previously active prairie dog colonies. We detected canine distemper, primarily in coyotes, in 14 of 15 years we sampled (Table 2.3, Figure 2.2) with only three samples analyzed in the single year without a detection. Average annual prevalence of canine distemper was $\bar{x} = 0.28 \pm 0.04$ (SE).

Evaluation of disease management

Non-dusted prairie dog colonies decreased in active area by 60.5% during each of the first three biennial mapping periods from 2007-13 when plague was present, compared to a 15.0% decrease in area of dusted colonies (Table 2.4, Figure 2.3, Appendix Figures S3-S9). Total area of non-dusted prairie dog colonies increased 49.0% compared to 12.7% on dusted colonies over each of the last two biennial periods from 2013-17.

The top-ranked models for black-footed ferret survival included age class, year, sex, dusting status, vaccination status, distance from known plague, and interactions between dusting status and distance from plague (Table 2.5). Estimated survival was highest in females and juveniles in all years, and during the plague epizootic it was highest for black-footed ferrets vaccinated with two doses, occupying dusted prairie dog colonies, and farther from known plague. Dusting status, distance to plague, and an interaction between the two covariates appeared in all top-ranked models, suggesting the relative importance of those variables may be greater than others. Models that included vaccination status without dusting status were not competitive. We used the second ranked model (Table 2.5) to estimate annual survival rates because that model included vaccination status. Estimated annual survival rates for both sexes and age classes declined precipitously with the invasion of plague, reaching the nadir in 2009, and then gradually increasing through 2013 before returning to pre-plague levels after 2014 (Tables 2.6-2.9, Figure 2.4). During 2007-2009, the period during the plague epizootic for which we had data on non-dusted/non-vaccinated ferrets and dusted/vaccinated ferrets (Table 2.2), dusting and vaccination with 2 doses improved annual black-footed ferret survival rates 49 to 116% over non-vaccinated ferrets that occupied non-dusted colonies. Dusting alone increased estimated annual survival rates for all sex and age classes, but increases in male survival (63-78%) were slightly greater than increases in female survival (49-73%). On dusted colonies, survival for black-footed ferrets with just one vaccination was approximately equivalent to non-vaccinated ferrets, but two vaccinations increased survival by 13-20% over non-vaccinated ferrets, emphasizing the value of two vaccine doses, even when applied across seasons. The survival of black-footed ferrets on dusted colonies did not depend on distance to plague, while the survival of ferrets occupying non-dusted colonies increased with distance to plague, becoming comparable to those on dusted colonies when >4 km from plague. Probability of capture, *p*, varied annually with survey effort and ranged from 0.33 – 0.97 (Figure 2.5). Annual MNA population estimates and primary period estimates increased prior to the invasion of plague in 2008, dramatically declined through 2013, and slowly increased again through 2016 (Table 2.10, Figure 2.6).

Discussion

Using carnivore serology, testing of prairie dog carcasses, and monitoring of prairie dog colony activity, we found no evidence of epizootic plague in the CB/BADL ecosystem from 1990-2007. Two coyotes tested positive during this period but we did not observe any large-scale mortality of prairie dogs indicative of epizootic plague (Matchett et al. 2010, Biggins et al. 2021). The plague positive coyote in 1994 may have been a long-distance immigrant from a known plague area in eastern Wyoming or a spurious test result (Williams et al. 1998). We suggest these two plague positive coyotes were not indicators of epizootic plague at CB/BADL. Although we cannot dismiss enzootic plague, it is unlikely in this case, as plague can be readily detected by carnivore serology even when present at low, enzootic levels. For instance, Matchett et al. (2010) used carnivore serology to conclude that plague was almost always present on their Montana prairie dog colonies after detecting plague-positive carnivores in 14 of 15 years sampled, with a mean prevalence of 55% and only six samples collected in the single year without a detection. The 2005 plague detection in a coyote in the CB/BADL area might have been associated with a plague epizootic in a prairie dog complex ~48 km south (Rocke et al. 2008) and an early indicator of the coming plague invasion. Our detection of plague in both carnivores and prairie dogs in 2008 was further confirmed by large-scale inactivity on large areas of prairie dog colonies. Past reports and observations of prairie dog inactivity were associated with poisoning, shooting, or drought (Bruggeman and Licht 2020), but plague is the only disease that is known to cause large-scale die-offs (Biggins et al. 2021). We conclude that the 2008 invasion of plague into CB/BADL was the first incursion of this disease.

Contrary to our plague results, we found canine distemper was commonly present in carnivores, primarily coyotes, at CB/BADL from 1990-2006. Despite the high susceptibility of black-footed ferrets to canine distemper, we did not observe any apparent decline in ferret populations that could be attributed to canine distemper. We did frequently vaccinate black-footed ferrets at CB/BADL against distemper, but the killed vaccines used early in these efforts may have been less effective than canarypox-vectored vaccines available after 2001 that produce higher titer levels (Wimsatt et al. 2006, Wright et al. 2022). Canine distemper transmission is typically by direct contact or fomites (Deem et al. 2000), but black-footed ferrets may not naturally contract the disease very often in the wild because it is short-lived in the environment. Direct transmission of canine distemper from coyotes to black-footed ferrets is unlikely because coyotes prey upon ferrets (Biggins et al. 2006b) and any contact is likely fatal for ferrets. The territorial nature of black-footed ferrets (Livieri and Anderson 2012) would reduce any opportunity for widespread transmission among ferrets. Undoubtedly, canine distemper is a risk to black-footed ferrets, particularly in captivity, but we suggest that the hazard to wild ferret populations may be minimal compared to the dual threat of direct mortality and habitat loss posed by plague. Black-footed ferrets are one of the oft-cited endangered species associated with canine distemper (Thorne and Williams 1988), but plague was the disease that largely contributed to historical range-wide declines of the species along with prairie dog poisoning and land conversion (U. S. Fish and Wildlife Service 2013, Livieri et al. 2022).

When plague reached CB/BADL in 2008, managers understood that flea vector control, through dusting prairie dog burrows, could protect both prairie dogs and black-footed ferrets, whereas the injectable vaccine would only protect ferrets (Matchett et al. 2010). Plague reduced prairie dog colony area on both dusted and non-dusted colonies for a minimum of five years after the initial detection of the epizootic (2008-2013) but the impact was more severe on non-dusted colonies, causing up to 65% reduction in colony area between mapping periods. Our annual dusting efforts preserved ~4,800 ha of colony area through the first five years of the epizootic while the area of non-dusted colonies fell sharply from 10,839.3 ha to 372.3 ha, an overall reduction of 96.6%, in that same period. If we had not dusted prairie dog colonies and allowed the plague epizootic to entirely invade the CB/BADL, it is likely that >90% of all the prairie dog colony area would have been impacted by plague, leading to extirpation of the black-footed ferret population.

Dusting with deltamethrin prevented the collapse of prairie dog colonies at CB/BADL, similar to results reported by Tripp et al. (2017) and Biggins et al. (2021), reducing overall plague transmission rates for both prairie dogs and black-footed ferrets while providing a somewhat stable prey base for ferrets compared to non-dusted areas. The area of dusted prairie dog colonies in the present study declined as much as 28.5% during the epizootic, suggesting that dusting is not 100% effective in protecting a prairie dog colony from plague; timing of annual dusting, human error, and flea resistance to deltamethrin may lessen the overall efficacy of this tool (Eads et al. 2018, Eads and Biggins 2019). Further refinements of dusting are needed for plague management, but dusting continues to be an effective tool for controlling fleas to maintain prairie dog populations (Biggins et al. 2021) and thus black-footed ferret populations.

Black-footed ferret annual survival dramatically decreased in 2008 and remained lower than pre-plague survival rates until 2014, coinciding with the invasion of plague and reduction in population size. In Montana, during enzootic plague circulating at low levels, vaccine dramatically increased survival of black-footed ferrets with effects equivalent to dusting (Matchett et al. 2010). However, during the observed plague epizootic at CB/BADL, dusting was more important than vaccination to black-footed ferret survival, increasing survival rates from 49-78% compared to ferrets occupying non-dusted areas, while two vaccinations were needed to additionally increase survival by 13-20% over dusting alone. For small populations of endangered animals even small increases in annual survival may make a difference between extirpation and recovery. Nevertheless, dusting or some form of effective vector control should continue to be the primary tool for managers to mitigate a plague epizootic, while vaccination of black-footed ferrets may be a secondary tool that provides incremental gains in ferret survival.

Our results demonstrate that epizootic plague may be monitored using carnivore serology and visual surveys, and that effective mitigation measures can be employed when epizootic plague is detected. However, it may be difficult for managers of smaller prairie dog complexes to mount a timely response to a plague epizootic because of the typically rapid spread of the disease (Biggins and Eads 2019). In the CB/BADL area there were >15,000 ha of active prairie dog colony prior to the detection of epizootic plague (2005-2007) and the disease impacted thousands of hectares in the first year (2008), yet we were able to dust nearly 5,000 hectares that were not yet impacted. Most prairie dog complexes where black-footed ferrets have been reintroduced are smaller in colony area than CB/BADL (Livieri et al. 2022), and the entire complex may be impacted before vector control can be employed; therefore, smaller ferret reintroduction areas should consider regular prophylactic dusting treatment of colonies. Black-footed ferret vaccination against plague should be administered whenever possible, particularly during the summer/fall seasons when population surveys are typically conducted in reintroduction areas. The combined efforts of vector control and vaccination of black-footed ferrets may be labor intensive but can be highly effective tools that are critically necessary for recovery of this endangered species.

Contributors

Coauthors on the anticipated publication from this chapter include Randall L. Griebel, Greg M. Schroeder, Doug Albertson, Dean E. Biggins, Tonie E. Rocke, William L. Kendall, Kevin R. Crooks, and Lisa M. Angeloni. The authors would like to thank the National Park Service, US Forest Service, US Fish and Wildlife Service, USDA APHIS Wildlife Services, US Geological Survey – Biological Resources Division, South Dakota Game, Fish and Parks, Defenders of Wildlife, World Wildlife Fund, Badlands Natural History Association, National Fish and Wildlife Foundation, and many other partners and supporters. David Jachowski, David Eads, and Shaun Grassel assisted with black-footed ferret spotlighting surveys. USDA APHIS Wildlife Services, South Dakota Game, Fish and Parks, and Sarah Bevins contributed to carnivore serosurveillance. US Fish and Wildlife Service and USDA APHIS Wildlife Services contributed to dusting prairie dog colonies. US Fish and Wildlife Service contributed to prairie dog activity surveys and carcass testing. The US Army Medical Research Institute of Infectious Diseases generously provided plague vaccine. Space prevents us from individually recognizing the hundreds of agency personnel, technicians, and volunteers who significantly contributed to this project over the years.

Table 2.1: Total prairie dog colony area and area treated with insecticide dust from 2005-2017 at Conata Basin/Badlands National Park, South Dakota.

Year	Total prairie dog colony area (ha)	Dusted active prairie dog colony area (ha)	# Dusted prairie dog burrows	Dusting dates (month/day)
2005	13,840.7	2,838.1	292,955	9/1 – 10/15
2006		549.0	93,867	9/5 – 10/20
2007	15,835.7	622.6	93,276	8/14 – 10/1
2008		4,385.2	453,560	6/2 – 9/16
2009	9,101.9	4,257.5	454,881	5/4 – 8/17
2010		4991.4	543,214	4/7 – 9/27
2011	5,130.3	3,889.0	478,398	4/5 – 9/7
2012		4,524.0	648,460	3/27 – 7/24
2013	4,287.3	4,018.2	545,320	4/29 – 8/23
2014		4,014.6	465,034	4/14 – 10/28
2015	4,042.0	3,608.1	499,765	3/18 – 9/16
2016		2,789.5	449,980	3/14 – 8/30
2017	5,524.6			

Table 2.2: Number of black-footed ferrets and plague treatments analyzed for survival using Program MARK. Ferrets resided on prairie dog colonies that were treated with insecticide dust and ferrets also received up to 2 doses of plague vaccine.

Year	Dusted – No Vax	Dusted – 1 vax	Dusted – 2 vax	No dust – No vax	No dust – 1 vax	No dust – 2 vax	# Adults (male.female)	# Juveniles (male.female)	Total
1998	0	0	0	40	0	0	8 (5.3)	32 (15.17)	40
1999	0	0	0	128	0	0	27 (10.17)	101 (46.55)	128
2000	0	0	0	151	0	0	70 (25.45)	81 (36.45)	151
2001	0	0	0	176	0	0	88 (29.59)	88 (45.43)	176
2002	0	0	0	182	0	0	84 (29.55)	98 (44.54)	182
2003	0	0	0	234	0	0	107 (36.71)	127 (58.69)	234
2004	0	0	0	192	0	0	101 (34.67)	91 (39.52)	192
2005	84	28	4	69	24	12	89 (37.52)	132 (57.75)	221
2006	20	16	6	133	29	10	100 (41.59)	114 (43.71)	214
2007	44	7	3	178	8	4	121 (43.78)	123 (56.67)	244
2008	24	84	33	3	42	2	97 (33.64)	91 (47.44)	188
2009	19	46	33	2	22	6	63 (17.46)	65 (31.34)	128
2010	14	58	15	0	8	1	34 (5.29)	62 (28.34)	96
2011	0	59	37	0	6	0	36 (7.29)	66 (32.34)	102
2012	0	42	42	0	6	3	41 (11.30)	52 (26.26)	93
2013	0	16	21	0	0	1	19 (6.13)	19 (6.13)	38
2014	0	26	44	0	3	3	25 (9.16)	51 (30.21)	76
2015	0	30	54	0	3	6	35 (17.18)	58 (27.31)	93
2016	0	49	52	0	4	9	43 (14.29)	71 (36.35)	114
Total	205	461	344	1,488	155	57	1,188 (408.780)	1,522 (702.820)	2,710

Table 2.3: Prevalence and 95% binomial exact confidence interval of plague and canine distemper in carnivores and rodents in the Conata Basin/Badlands National Park, South Dakota, 1990-2009. Other category includes raccoon, red fox, swift fox, and bobcats.

Year	Plague prevalence							Canine distemper prevalence					
	Coyote	Badger	Skunk	Prairie dog	Other	Total	Total % prevalence (95% CI)	Coyote	Badger	Skunk	Other	Total	Total % prevalence (95% CI)
1990	0/36	0/15	0/18		0/11	0/80	0.0 (0.0-0.05)	8/37	1/15	0/18	0/11	9/81	0.01 (0.05-0.20)
1993	0/21	0/39	0/8		0/16	0/84	0.0 (0.0-0.04)	6/19	0/41	0/7	1/17	7/84	0.08 (0.03-0.16)
1994	1/21	0/13	0/8	0/9	0/2	1/51	0.02 (0.0-0.10)	2/21	1/13	0/7	0/2	3/43	0.07 (0.01-0.19)
1995	0/10	0/12	0/8	0/33		0/63	0.0 (0.0-0.06)	7/10	0/12	0/5		7/27	0.26 (0.11-0.46)
1996	0/11			0/29		0/40	0.0 (0.0-0.09)	6/11				6/11	0.55 (0.23-0.83)
1997	0/35	0/9		0/21	0/3	0/68	0.0 (0.0-0.05)	18/35	0/9		0/3	18/47	0.38 (0.24-0.54)
1998	0/21	0/3				0/24	0.0 (0.0-0.14)	9/19	0/3			9/22	0.41 (0.21-0.64)
1999	0/18	0/3			0/1	0/22	0.0 (0.0-0.15)	5/18	0/3		0/1	5/22	0.23 (0.08-0.45)
2000	0/3					0/3	0.0 (0.0-0.71)	0/3				0/3	0.0 (0.0-0.71)
2001	0/10		0/1			0/11	0.0 (0.0-0.28)	3/10		0/1		3/11	0.27 (0.06-0.61)
2002	0/43		0/1	0/1	0/1	0/46	0.0 (0.0-0.08)	16/43				16/43	0.37 (0.23-0.53)
2003	0/69				0/1	0/70	0.0 (0.0-0.05)	16/69				16/69	0.23 (0.14-0.35)
2004	0/61					0/61	0.0 (0.0-0.06)	21/61				21/61	0.34 (0.23-0.48)
2005	1/67					1/67	0.01 (0.0-0.08)	9/27				9/27	0.33 (0.17-0.54)
2006	0/57					0/57	0.0 (0.0-0.06)	3/5				3/5	0.60 (0.15-0.95)
2007	0/29	0/2		0/3		0/34	0.0 (0.0-0.10)						
2008	3/29			7/10	3/61	13/100	0.13 (0.07-0.21)						
2009	1/18	4/16		4/5		9/39	0.23 (0.11-0.39)						

Table 2.4: Size (hectares) of prairie dog colonies with and without treatment of insecticide dust, with the total colony area at the start and end of each 2-year colony mapping interval.

Year interval	Treatment	# colonies	Mean colony size (ha) ±SE	Range (ha)	Total area (ha) start	Total area (ha) end	% change in total area (ha)
2007-09	Dust	8	601.6 ±173.3	228.3 – 1,571.1	4,812.8	4,626.6	-3.9%
2007-09	No dust	115	94.3 ±23.9	0.5 – 1,769.1	10,839.3	4,275.4	-60.6%
2009-11	Dust	18	286.3 ±96.8	2.2 – 1,538.5	5,153.8	3,687.1	-28.5%
2009-11	No dust	97	38.7 ±7.6	0.2 – 560.0	3,750.8	1,285.7	-65.7%
2011-13	Dust	49	94.0 ±27.6	0.6 – 1,103.2	4,605.4	4,023.3	-12.6%
2011-13	No dust	56	6.6 ±1.4	0.1 – 41.5	372.3	166.7	-55.2%
2013-15	Dust	44	91.4 ±26.5	0.1 – 1,062.6	4,021.1	3,724.0	-7.4%
2013-15	No dust	44	3.9 ±1.6	0.2 – 66.6	173.7	218.9	+26.0%
2015-17	Dust	47	76.9 ±24.5	1.0 – 1,067.6	3,616.4	4,797.3	+32.7%
2015-17	No dust	38	9.1 ±3.7	0.2 – 124.7	343.9	591.0	+71.9%

Table 2.5: Full set of models evaluated using the Barker model for annual black-footed ferret survival at Conata Basin/Badlands National Park, South Dakota, 1998-2017. The top competitive models are in italics.

Model[1]	**AICc**	**Δ AICc**	**AICc Weight**	**K**	**Deviance**
S(a, t, sex, dust, plague, dust*plague) p(t, effort) R(t) R'(t)	6073.4	0	0.46	72	5927.4
S(a, t, sex, dust, vx1, vx2, plague, dust*plague) p(t, effort) R(t) R'(t)	6074.8	1.4	0.23	74	5924.7
S(a, t, sex, dust, vx1, plague, dust*plague) p(t, effort) R(t) R'(t)	6075.4	2.0	0.17	73	5927.4
S(a, t, sex, dust, vx1, plague, dust*plague*vx1) p(t, effort) R(t) R'(t)	6075.9	2.5	0.13	74	5925.8
S(a, t, sex, dust, plague) p(t, effort) R(t) R'(t)	6083.3	9.9	0.00	71	5939.4
S(a, t, sex, dust, vx1, vx2, plague) p(t, effort) R(t) R'(t)	6084.5	11.1	0.00	73	5936.5
S(a, t, sex, dust, vx1, plague) p(t, effort) R(t) R'(t)	6085.3	11.9	0.00	72	5939.4
S(a, t, sex, dust, vx1, plague, vx1*plague) p(t, effort) R(t) R'(t)	6085.4	12.0	0.00	73	5937.4
S(a, t, g, plague) p(t, effort) R(t) R'(t)	6086.1	12.7	0.00	70	5944.3
S(a, t, sex, vx1, vx2, plague) p(t, effort) R(t) R'(t)	6087.1	13.7	0.00	72	5941.1
S(a, t, sex, vx1, plague) p(t, effort) R(t) R'(t)	6088.1	14.7	0.00	71	5944.2
S(a, t, sex, dust) p(t, effort) R(t) R'(t)	6110.2	36.8	0.00	70	5968.4
S(a, t, sex) p(t, effort) R(t) R'(t)	6112.1	38.7	0.00	69	5972.3
S(a, t, sex, vx1, vx2) p(t, effort) R(t) R'(t)	6113.8	40.4	0.00	71	5969.9
S(a, t, sex, vx1) p(t, effort) R(t) R'(t)	6114.0	40.6	0.00	70	5972.1
S(a, t, sex) p(t, g, effort) R(t) R'(t)	6114.5	41.1	0.00	69	5974.7
S(a ,t, sex) p(t) R(t) R'(t)	6114.6	41.2	0.00	66	5980.9
S(a, t, sex) p(a, t, effort) R(t) R'(t)	6115.2	41.8	0.00	69	5975.4
S(a, t, sex) p(a, t) R(t) R'(t)	6116.5	43.1	0.00	67	5980.8
S(a, t, sex) p(t, effort) R(t) R'(t)	6116.6	43.2	0.00	68	5978.9
S(a, t, sex) p(t, g) R(t) R'(t)	6122.6	49.2	0.00	67	5986.8
S(a, t) p(t) R(t) R'(t)	6182.7	109.3	0.00	65	6051.1
S(t) p(t) R(t) R'(t)	6183.4	110.0	0.00	65	6051.8
S(t) p(.) R(t) R'(t)	6249.2	175.8	0.00	52	6144.1
S(.) p(.) R(.) R'(.)	7450.9	1377.5	0.00	4	7442.9

[1] Parameters include survival (S), probability of capture (p), a = age, t = year, dust = dusted, plague = distance from plague, vx1 = 1 dose of plague vaccine, vx2 = 2 or more doses of plague vaccine, effort = spotlighting effort, (.) = constant. F=1 and r=0 for all models.

Table 2.6: Estimated annual survival (bold), standard error, and 95% confidence intervals for adult female black-footed ferrets at Conata Basin/Badlands National Park, South Dakota, 1998-2016 with no plague management (no dust, no vaccine), insecticide dust only, dust and 1 vaccination, and dust with 2 vaccinations.

Year	**Survival** (SE), 95% confidence interval			
	No dust, no vaccine	Dust only	Dust, 1 vaccine	Dust, 2 vaccine
1998	**0.57** (0.08), 0.41-0.72			
1999	**0.58** (0.05), 0.48-0.67			
2000	**0.55** (0.04), 0.46-0.64			
2001	**0.51** (0.04), 0.43-0.59			
2002	**0.59** (0.04), 0.51-0.66			
2003	**0.51** (0.05), 0.42-0.60			
2004	**0.44** (0.05), 0.35-0.54			
2005	**0.41** (0.05), 0.32-0.52			
2006	**0.48** (0.05), 0.39-0.57			
2007	**0.23** (0.04), 0.16-0.31	**0.35** (0.05), 0.26-0.46	**0.34** (0.06), 0.23-0.47	**0.40** (0.07), 0.28-0.54
2008	**0.21** (0.05), 0.13-0.32	**0.33** (0.06), 0.22-0.46	**0.32** (0.05), 0.23-0.42	**0.38** (0.06), 0.27-0.50
2009	**0.07** (0.03), 0.03-0.16	**0.13** (0.05), 0.06-0.25	**0.12** (0.04), 0.06-0.23	**0.15** (0.05), 0.08-0.29
2010		**0.37** (0.10), 0.20-0.57	**0.35** (0.09), 0.20-0.54	**0.42** (0.10), 0.24-0.62
2011			**0.26** (0.06), 0.16-0.40	**0.32** (0.07), 0.21-0.46
2012			**0.47** (0.11), 0.27-0.67	**0.53** (0.10), 0.35-0.71
2013			**0.30** (0.08), 0.17-0.48	**0.36** (0.09), 0.21-0.54
2014			**0.49** (0.08), 0.33-0.65	**0.56** (0.08), 0.40-0.70
2015			**0.52** (0.09), 0.35-0.68	**0.59** (0.08), 0.43-0.73
2016			**0.68** (0.12), 0.41-0.87	**0.74** (0.11), 0.48-0.90

Table 2.7: Estimated annual survival (bold), standard error, and 95% confidence intervals for juvenile female black-footed ferrets at Conata Basin/Badlands National Park, South Dakota, 1998-2016 with no plague management (no dust, no vaccine), insecticide dust only, dust and 1 vaccination, and dust with 2 vaccinations.

Year	**Survival** (SE), 95% confidence interval			
	No dust, no vaccine	Dust only	Dust, 1 vaccine	Dust, 2 vaccine
1998	**0.63** (0.08), 0.47-0.76			
1999	**0.64** (0.05), 0.54-0.72			
2000	**0.61** (0.04), 0.52-0.69			
2001	**0.57** (0.04), 0.49-0.65			
2002	**0.65** (0.04), 0.57-0.72			
2003	**0.57** (0.05), 0.48-0.66			
2004	**0.50** (0.05), 0.40-0.60			
2005	**0.47** (0.05), 0.37-0.58			
2006	**0.54** (0.05), 0.44-0.63			
2007	**0.27** (0.04), 0.20-0.37	**0.41** (0.05), 0.31-0.52	**0.39** (0.07), 0.27-0.53	**0.46** (0.08), 0.32-0.61
2008	**0.25** (0.06), 0.16-0.38	**0.39** (0.07), 0.26-0.52	**0.37** (0.06), 0.27-0.48	**0.44** (0.07), 0.31-0.57
2009	**0.09** (0.04), 0.04-0.20	**0.16** (0.06), 0.07-0.30	**0.15** (0.05), 0.07-0.28	**0.19** (0.06), 0.09-0.34
2010		**0.42** (0.11), 0.24-0.63	**0.41** (0.10), 0.24-0.60	**0.47** (0.11), 0.28-0.68
2011			**0.31** (0.06), 0.20-0.45	**0.37** (0.07), 0.25-0.52
2012			**0.52** (0.11), 0.32-0.72	**0.59** (0.10), 0.40-0.76
2013			**0.35** (0.09), 0.20-0.54	**0.42** (0.09), 0.25-0.60
2014			**0.55** (0.08), 0.39-0.70	**0.62** (0.08), 0.46-0.75
2015			**0.58** (0.08), 0.41-0.73	**0.64** (0.08), 0.48-0.78
2016			**0.73** (0.11), 0.47-0.89	**0.78** (0.10), 0.54-0.92

Table 2.8: Estimated annual survival (bold), standard error, and 95% confidence intervals for adult male black-footed ferrets at Conata Basin/Badlands National Park, South Dakota, 1998-2016 with no plague management (no dust, no vaccine), insecticide dust only, dust and 1 vaccination, and dust with 2 vaccinations.

Year	**Survival** (SE), 95% confidence interval			
	No dust, no vaccine	Dust only	Dust, 1 vaccine	Dust, 2 vaccine
1998	**0.39** (0.08), 0.25-0.56			
1999	**0.40** (0.05), 0.31-0.50			
2000	**0.37** (0.04), 0.29-0.46			
2001	**0.34** (0.04), 0.26-0.42			
2002	**0.41** (0.04), 0.33-0.49			
2003	**0.33** (0.04), 0.26-0.42			
2004	**0.28** (0.04), 0.20-0.37			
2005	**0.25** (0.04), 0.18-0.35			
2006	**0.31** (0.04), 0.23-0.39			
2007	**0.13** (0.03), 0.08-0.18	**0.21** (0.04), 0.14-0.29	**0.20** (0.04), 0.13-0.30	**0.25** (0.05), 0.15-0.37
2008	**0.12** (0.03), 0.07-0.19	**0.19** (0.04), 0.12-0.30	**0.18** (0.04), 0.12-0.26	**0.23** (0.05), 0.15-0.33
2009	**0.04** (0.02), 0.02-0.09	**0.07** (0.03), 0.03-0.14	**0.06** (0.02), 0.03-0.13	**0.08** (0.03), 0.04-0.16
2010		**0.22** (0.07), 0.11-0.40	**0.21** (0.07), 0.11-0.37	**0.26** (0.08), 0.13-0.45
2011			**0.15** (0.04), 0.09-0.24	**0.19** (0.05), 0.11-0.29
2012			**0.30** (0.07), 0.17-0.46	**0.36** (0.10), 0.19-0.57
2013			**0.17** (0.05), 0.09-0.30	**0.21** (0.07), 0.11-0.37
2014			**0.32** (0.07), 0.19-0.47	**0.38** (0.07), 0.25-0.53
2015			**0.34** (0.08), 0.21-0.51	**0.41** (0.08), 0.26-0.57
2016			**0.51** (0.14), 0.25-0.76	**0.58** (0.14), 0.30-0.81

Table 2.9: Estimated annual survival (bold), standard error, and 95% confidence intervals for juvenile male black-footed ferrets at Conata Basin/Badlands National Park, South Dakota, 1998-2016 with no plague management (no dust, no vaccine), insecticide dust only, dust and 1 vaccination, and dust with 2 vaccinations.

Year	**Survival** (SE), 95% confidence interval			
	No dust, no vaccine	Dust only	Dust, 1 vaccine	Dust, 2 vaccine
1998	**0.45** (0.08), 0.30-0.61			
1999	**0.46** (0.05), 0.37-0.55			
2000	**0.43** (0.05), 0.34-0.52			
2001	**0.39** (0.04), 0.31-0.47			
2002	**0.47** (0.04), 0.39-0.55			
2003	**0.39** (0.05), 0.30-0.48			
2004	**0.33** (0.05), 0.24-0.43			
2005	**0.30** (0.05), 0.22-0.40			
2006	**0.36** (0.05), 0.28-0.45			
2007	**0.15** (0.03), 0.11-0.22	**0.25** (0.04), 0.18-0.34	**0.24** (0.05), 0.15-0.35	**0.29** (0.06), 0.18-0.43
2008	**0.14** (0.04), 0.08-0.23	**0.23** (0.05), 0.15-0.35	**0.22** (0.04), 0.15-0.31	**0.27** (0.05), 0.18-0.39
2009	**0.05** (0.02), 0.02-0.11	**0.08** (0.03), 0.04-0.17	**0.08** (0.03), 0.04-0.16	**0.10** (0.04), 0.05-0.20
2010		**0.26** (0.09), 0.13-0.46	**0.25** (0.08), 0.13-0.43	**0.30** (0.09), 0.15-0.51
2011			**0.18** (0.04), 0.11-0.28	**0.22** (0.05), 0.14-0.35
2012			**0.35** (0.08), 0.21-0.52	**0.41** (0.11), 0.22-0.63
2013			**0.21** (0.06), 0.11-0.36	**0.26** (0.08), 0.13-0.44
2014			**0.37** (0.08), 0.24-0.53	**0.44** (0.08), 0.29-0.59
2015			**0.40** (0.08), 0.25-0.56	**0.46** (0.08), 0.31-0.63
2016			**0.57** (0.14), 0.30-0.80	**0.63** (0.13), 0.36-0.84

Table 2.10: Annual black-footed ferret minimum number alive (MNA) population estimates, number of PIT-tagged ferrets identified during the late summer/fall primary period, and estimated population size during the primary period using *p*, probability of detection in Conata Basin/Badlands National Park, South Dakota from 1999-2016.

Year	Minimum number alive (MNA)	Number identified during primary period	Primary period population estimate
1999	206	167	189
2000	242	195	222
2001	210	186	201
2002	210	191	197
2003	296	266	276
2004	231	194	260
2005	276	247	324
2006	286	204	315
2007	355	280	442
2008	257	213	323
2009	187	140	213
2010	126	81	170
2011	119	72	119
2012	100	68	92
2013	49	30	92
2014	78	43	57
2015	95	90	127
2016	125	114	156

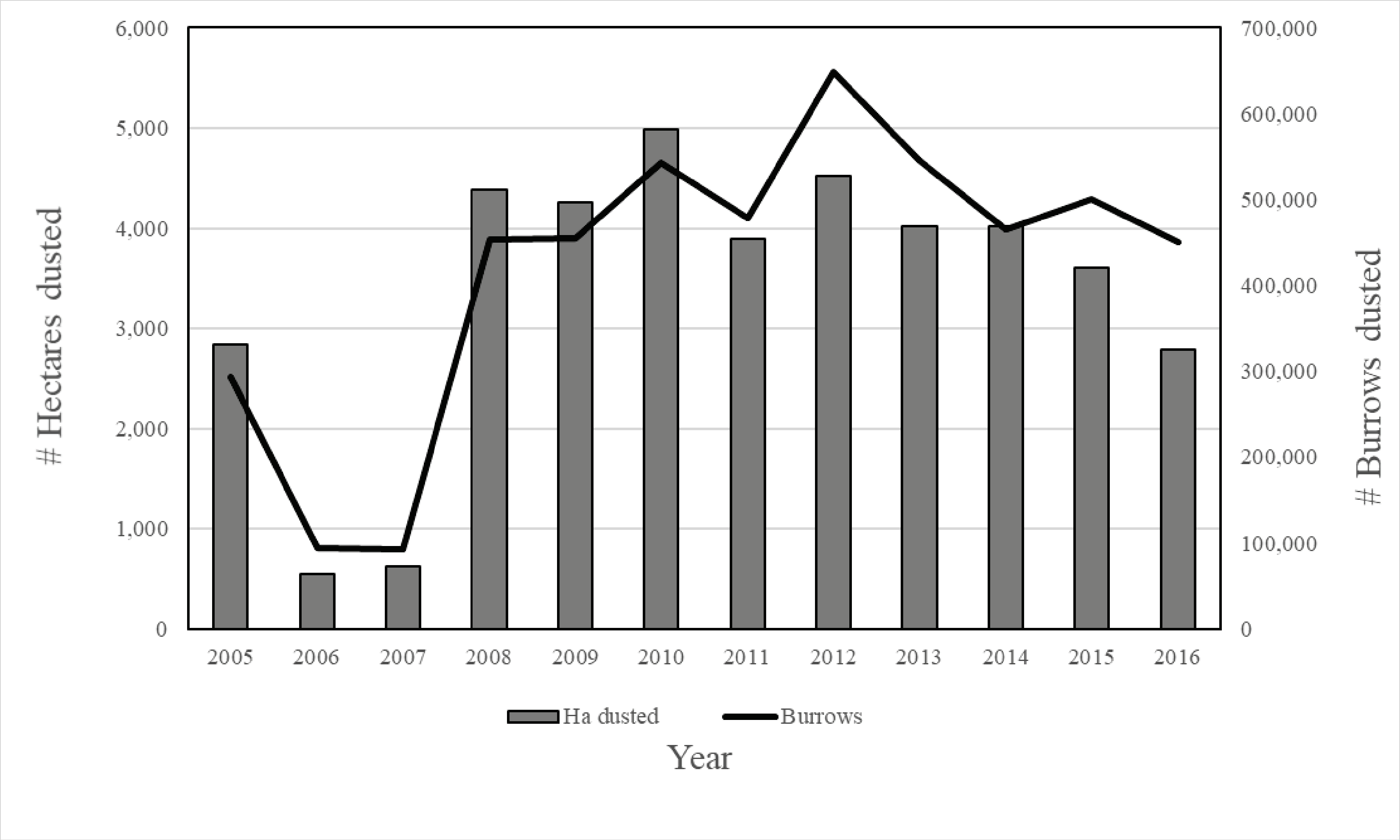

Figure 2.1: Prairie dog colony area (ha) treated with insecticide dust and number of prairie dog burrows annually treated 2005-16 at Conata Basin/Badlands National Park, South Dakota.

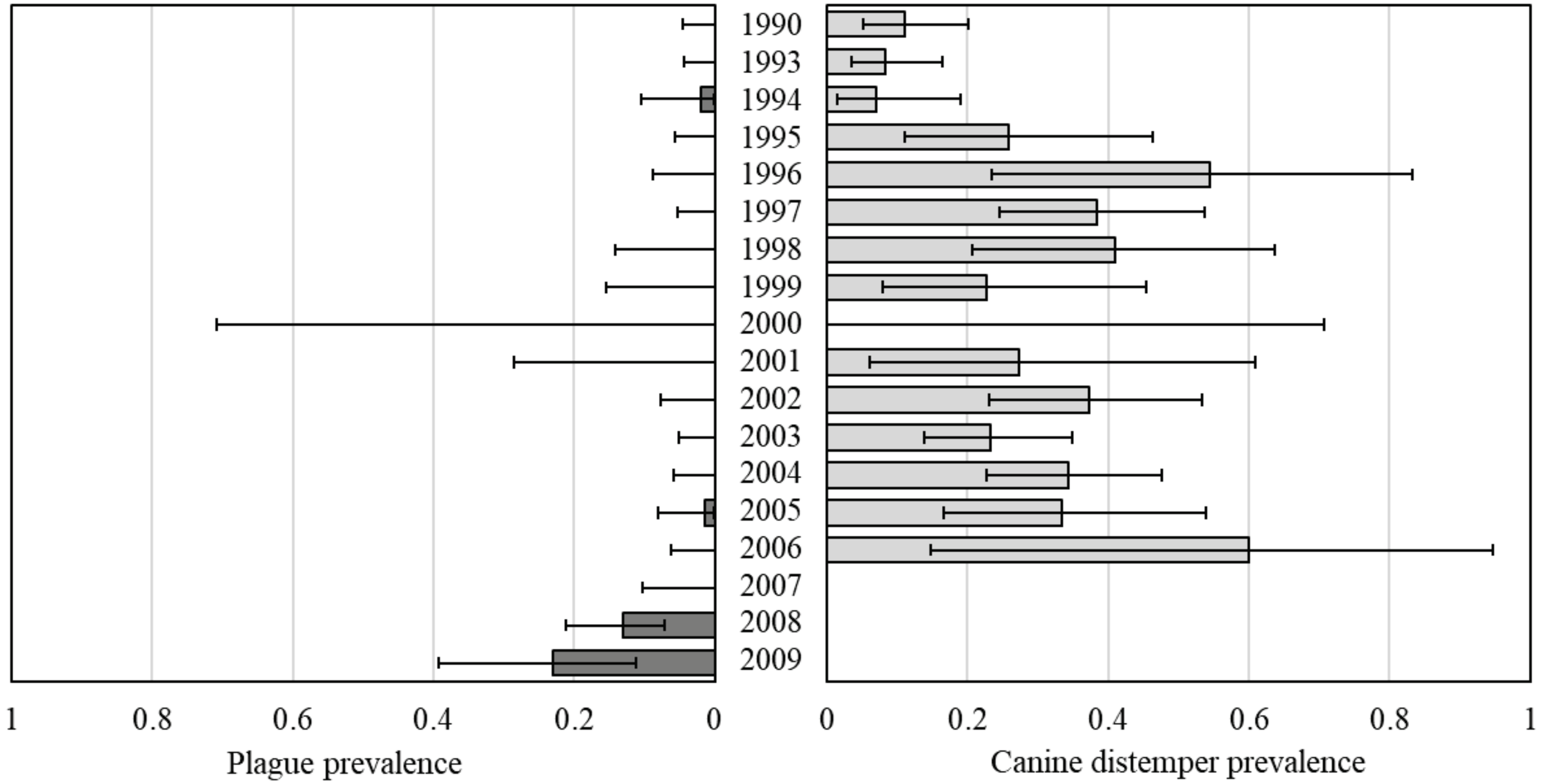

Figure 2.2: Annual estimated prevalence with 95% confidence intervals of plague and canine distemper seroprevalence in carnivores and black-tailed prairie dogs (plague only) in Conata Basin/Badlands National Park, South Dakota, 1990-2009. No sampling for canine distemper occurred 2007-2009.

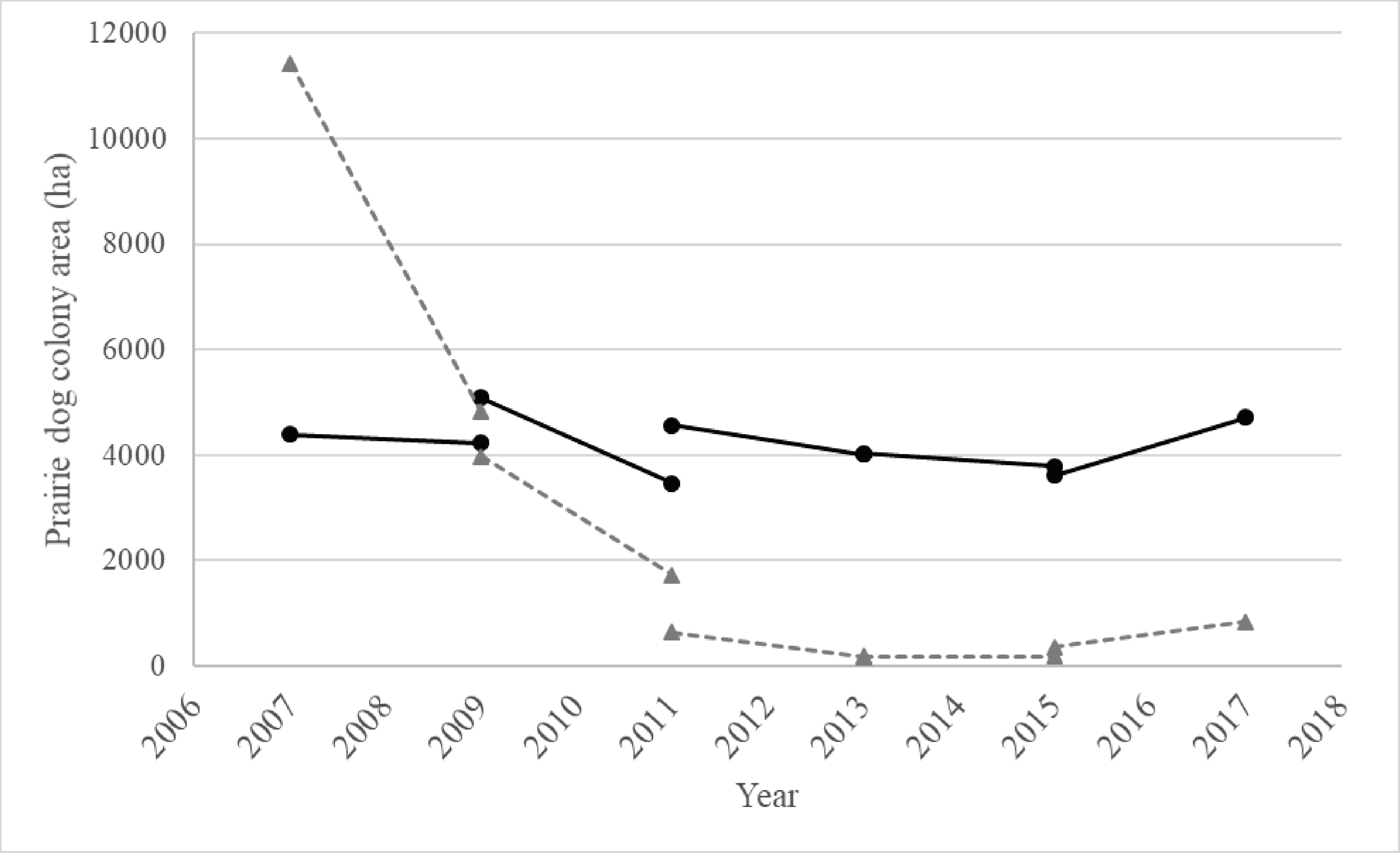

Figure 2.3: Effect of annual dust application on prairie dog colony area during a plague epizootic in Conata Basin/Badlands National Park, South Dakota, 2007-2017. Colonies dusted at least once during a bi-annual period (solid black lines) maintained area compared to colonies without any insecticide dusting (dashed gray lines).

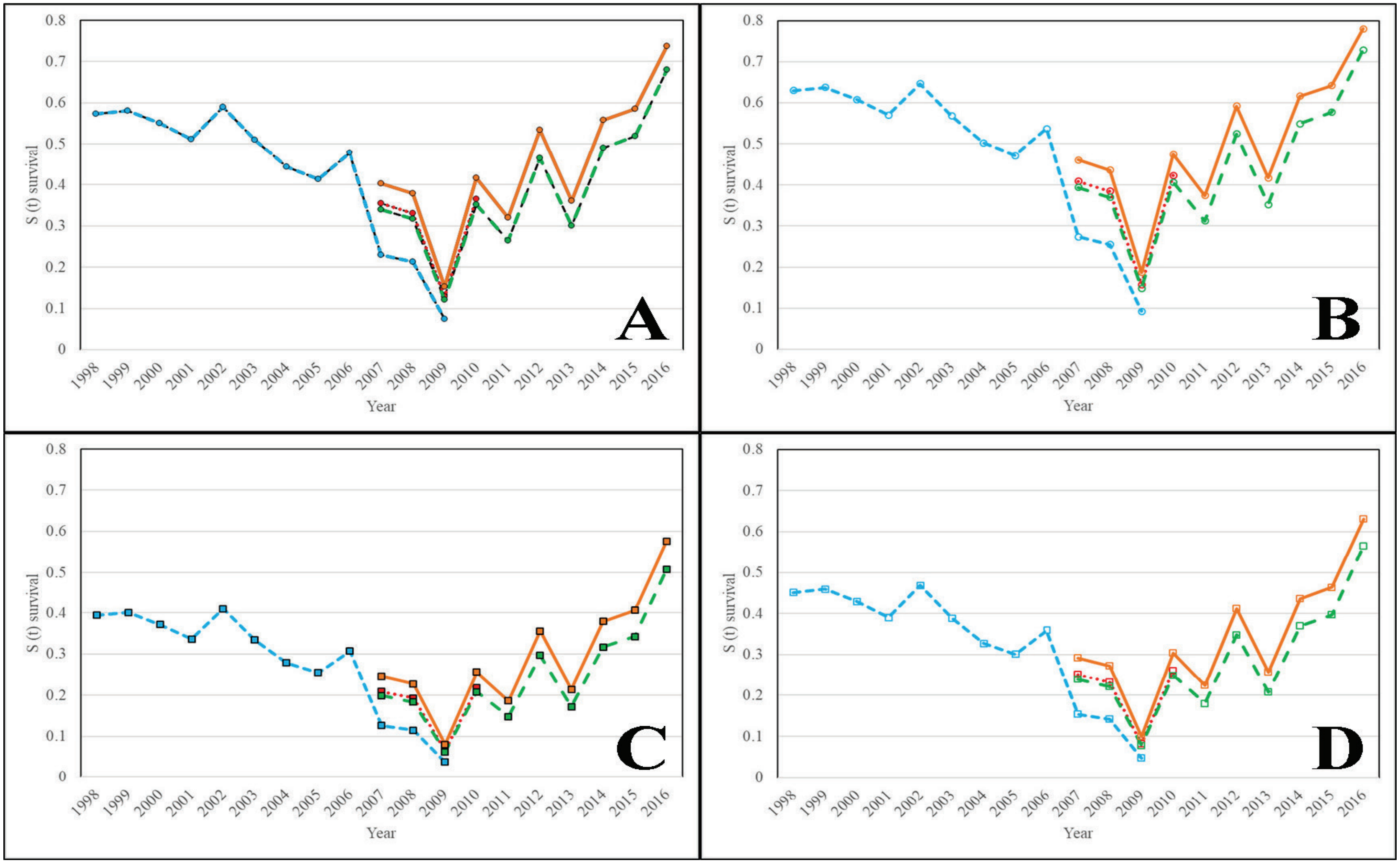

Figure 2.4: Annual survival rates (S) of female adult (A), female juvenile (B), male adult (C), and male juvenile (D) black-footed ferrets at Conata Basin/Badlands National Park, South Dakota, 1998-2016 in relation to dusting, vaccination. The lower dashed line indicates survival rates for non-vaccinated ferrets occupying non-dusted prairie dog colonies. The middle dashed line indicates survival rates for ferrets with one vaccination occupying dusted colonies. The dotted line indicates survival rates of non-vaccinated ferrets occupying dusted colonies. The solid line indicates survival rates for ferrets with two vaccinations occupying dusted colonies.

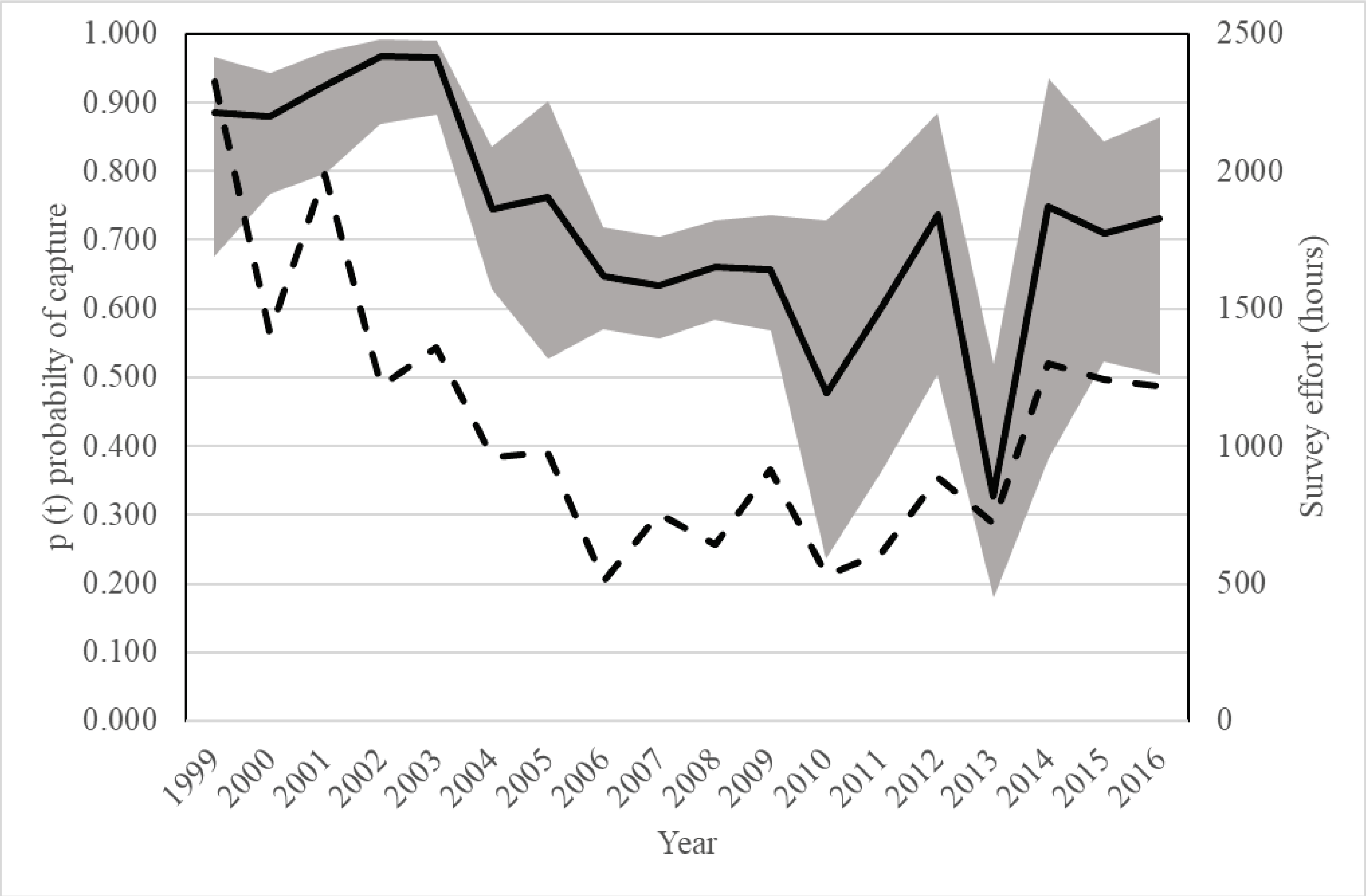

Figure 2.5: Annual estimated probability of capture (p; solid line with shaded 95% confidence interval) for black-footed ferrets at Conata Basin/Badlands National Park, South Dakota, 1999-2016. Survey effort (hours of spotlighting; dashed line) during the primary period are plotted on the secondary vertical axis for comparison.

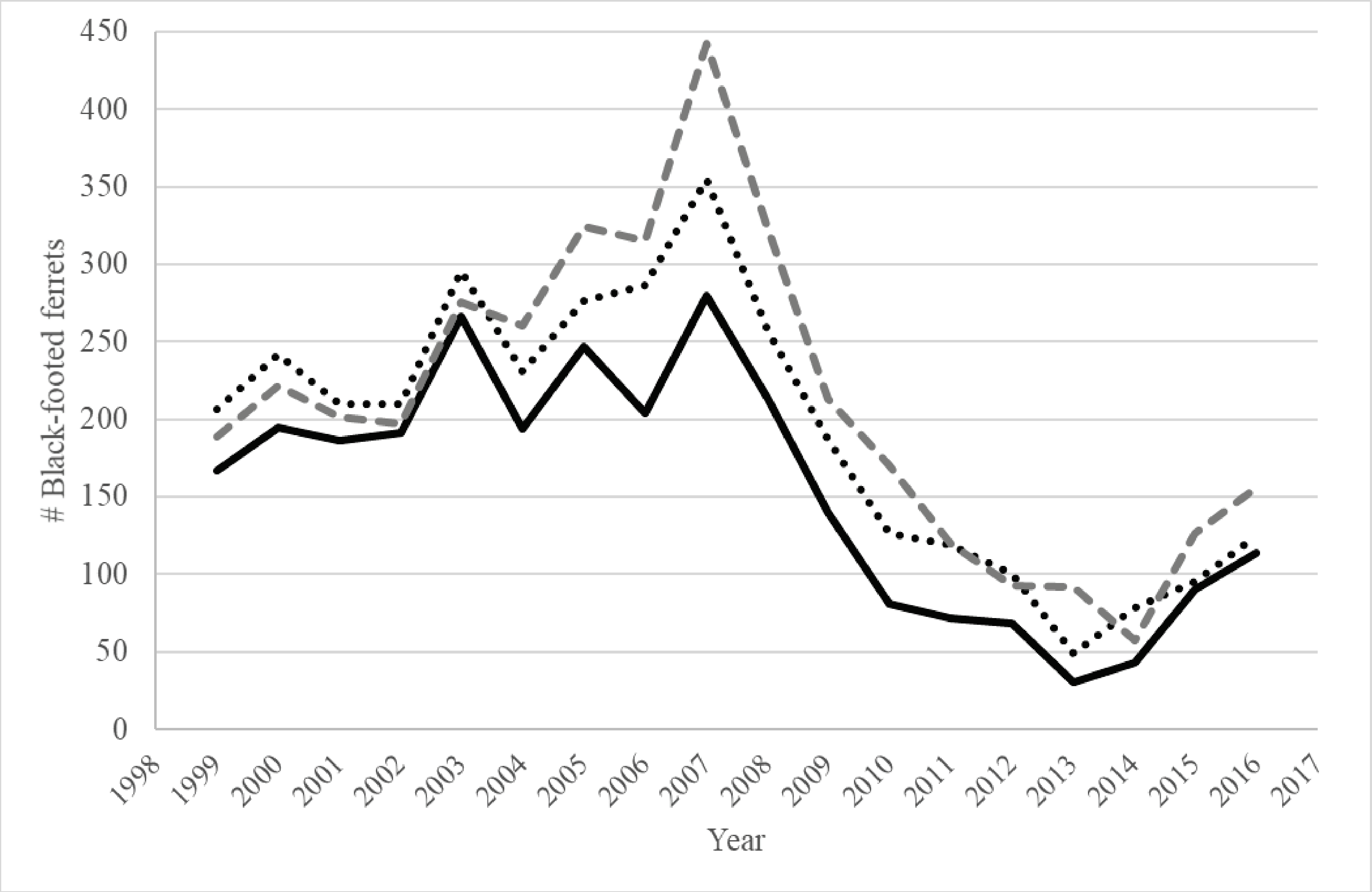

Figure 2.6: Estimated annual black-footed ferret population size in Conata Basin/Badlands National Park, South Dakota from 1999-2016. We used minimum number alive (MNA; dotted black line), number identified during the primary period (solid black line), and estimated primary period population size using annual detection probabilities (dashed gray line) to estimate population size.

REFERENCES

Antolin, M. F., P. Gober, B. Luce, D. E. Biggins, W. E. Van Pelt, D. B. Seery, M. Lockhart, and M. Ball. 2002. The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. Transactions of the 67th North American Wildlife and Natural Resources Conference 67:104-127. https://digitalcommons.unl.edu/usfwspubs/57/

Artois, M., R. Bengis, R. J. Delahay, M. J. Duchene, J. P. Duff, E. Ferroglio, C. Gortazar, M. R. Hutchings, R. A. Kock, F. A. Leighton, T. Morner, and G. C. Smith. 2009. Wildlife disease surveillance and monitoring. Pages 187-214 in R. J. Delahay, G. C. Smith, and M. R. Hutchings, editors. Management of disease in wild mammals. Springer, Tokyo, Japan. https://doi.org/10.1007/978-4-431-77134-0_10

Barker, R. J., K. P. Burnham, and G. C. White. 2004. Encounter history modeling of joint mark-recapture, tag-resighting and tag recovery data under temporary emigration. Statistica Sinica 14:1037-1055. https://www.jstor.org/stable/24307217

Barnes, A. M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pages 28-37 in J. L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, editors. Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. US Fish and Wildlife Service Biological Report No. 13. Washington, D. C. https://pubs.usgs.gov/fedgov/70039171/report.pdf#page=32

Biggins, D. E., and D. A. Eads. 2019. Prairie dogs, persistent plague, flocking fleas, and pernicious positive feedback. Frontiers in Veterinary Science 6:75. https://doi.org/10.3389/fvets.2019.00075

Biggins, D. E., J. L. Godey, and D. A. Eads. 2021. Epizootic plague in prairie dogs: correlates and control with deltamethrin. Vector-Borne and Zoonotic Diseases 21:172-178. https://doi.org/10.1089/vbz.2020.2684

Biggins, D. E., J. L. Godbey, K. L. Gage, L. G. Carter, and J. A. Montenieri. 2010. Vector control improves survival of prairie dogs (*Cynomys*) in areas considered enzootic for plague. Vector-Borne and Zoonotic Diseases 10:17-26. https://doi.org/10.1089/vbz.2009.0049

Biggins, D. E., J. L. Godbey, L. R. Hanebury, B. Luce, P. E. Marinari, M. R. Matchett, and A. Vargas. 1998. The effect of rearing methods on survival of reintroduced black-footed ferrets. Journal of Wildlife Management 62:643-653. https://doi.org/10.2307/3802340

Biggins, D. E., J. L. Godbey, M. R. Matchett, L. R. Hanebury, T. M. Livieri, and P. E. Marinari. 2006a. Monitoring black-footed ferrets during reestablishment of free-ranging populations: discussion of alternative methods and recommended minimum standards. Pages 155-174 in J.E. Roelle, B.J. Miller, J.L. Godbey, and D.E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://pubs.usgs.gov/publication/70180911

Biggins, D. E., J. L. Godbey, T. M. Livieri, M. R. Matchett, and B. D. Bibles. 2006b. Postrelease movements and survival of adult and young black-footed ferrets. Pages 191-200 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://pubs.usgs.gov/publication/70180912

Biggins, D. E., J. L. Godbey, M. R. Matchett and T. M. Livieri. 2006c. Habitat preferences and intraspecific competition in black-footed ferrets. Pages 129-140 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://pubs.usgs.gov/publication/70180909

Biggins, D. E., and M. Y. Kosoy. 2001. Influences of introduced plague on North American mammals: implications from ecology of plague in Asia. Journal of Mammalogy 82:906-916. https://doi.org/10.1644/1545-1542(2001)082<0906:IOIPON>2.0.CO;2

Biggins, D. E., J. G. Sidle, D. B. Seery, and A. E. Ernst. 2006d. Estimating the abundance of prairie dogs. Pages 94-107 in J. L. Hoogland, editor. Conservation of the black-tailed prairie dog: saving North America's western grasslands. Island Press, Washington D. C.

Black-Footed Ferret Recovery Implementation Team. 2016. Black-footed ferret field operations manual. U. S. Fish and Wildlife Service, Wellington, Colorado. https://www.fws.gov/sites/default/files/documents/black-footed-ferret-field-operations-manual-2016.pdf

Breed, A. C., R. K. Plowright, D. T. S. Hayman, D. L. Knobel, F. M. Molenaar, D. Gardner-Roberts, S. Cleaveland, D. T. Haydon, R. A. Kock, A. A. Cunningham, A. W. Sainsbury, and R. J. Delahay. 2009. Disease management in endangered mammals. Pages 215-239 in R. J. Delahay, G. C. Smith, and M. R. Hutchings, editors. Management of disease in wild mammals. Springer, Tokyo, Japan. https://doi.org/10.1007/978-4-431-77134-0_11

Bruggeman, J. E., and D. S. Licht. 2020. Drought-mediated changes in black-tailed prairie dogs colonies in the Northern Great Plains. Journal of Mammalogy 101:1189-1204. https://doi.org/10.1093/jmammal/gyaa070

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociological Methods & Research 33:261-304. https://doi.org/10.1177/0049124104268644

Carpenter, J. W., M. J. Appel, R. C. Erickson, and M. N. Novilla. 1976. Fatal vaccine-induced canine distemper virus infection in black-footed ferrets. Journal of the American Veterinary Medical Association 169:961-964. https://europepmc.org/article/med/988011

Chades, I., T. G. Martin, S. Nicol, M. A. Burgman, H. P. Possingham, and Y. M. Buckley. 2011. General rules for managing and surveying networks of pests, diseases, and endangered species. Proceedings of the National Academy of Sciences 108:8323-8328. https://doi.org/10.1073/pnas.1016846108

Cleaveland, S. 2009. Viral threats and vaccination: disease management of endangered species. Animal Conservation 12:187-189. http://dx.doi.org/10.1111/j.1469-1795.2009.00276.x

Clifford, D. L., J. A. K. Mazet, E. J. Dubovi, D. K. Garcelon, T. J. Coonan, P. A. Conrad, and L. Munson. 2006. Pathogen exposure in endangered island fox (*Urocyon littoralis*) populations: Implications for conservation and management. Biological Conservation 131:230-243. https://doi.org/10.1016/j.biocon.2006.04.029

Collinge, S. K., C. Ray, and J. F. Cully, Jr. 2008. Effects of disease on keystone species, dominant species, and their communities. Pages 129-144 in R. S. Ostfeld, F. Keesing, and V. T. Eviner, editors. Infectious disease ecology: the effects of ecosystems on disease and of disease on ecosystems. Prineceton University Press, Princeton, New Jersey.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife

– threats to biodiversity and human health. Science 287:443-449. https://doi.org/10.1126/science.287.5452.443

de Castro, F., and B. Bolker. 2005. Mechanisms of disease-induced extinction. Ecology Letters 8:117-126. https://doi.org/10.1111/j.1461-0248.2004.00693.x

Deem, S. L., L. H. Spelman, R. A. Yates, and R. J. Montali. 2000. Canine distemper in terrestrial carnivores: a review. Journal of Zoo and Wildlife Medicine 31:441-451. https://doi.org/10.1638/1042-7260(2000)031[0441:CDITCA]2.0.CO;2

Delahay, R. J., G. C. Smith, and M. R. Hutchings. 2009. The science of wildlife disease management. Pages 1-8 in R. J. Delahay, G. C. Smith, and M. R. Hutchings, editors. Management of disease in wild mammals. Springer, Tokyo, Japan. https://doi.org/10.1007/978-4-431-77134-0_1

Ducatez, S., and R. Shine. 2017. Drivers of extinction risk in terrestrial vertebrates. Conservation Letters 10:186-194. https://doi.org/10.1111/conl.12258

Eads, D. A., and D. E. Biggins. 2015. Plague bacterium as a transformer species in prairie dogs and the grasslands of western North America. Conservation Biology 29:1086-1093. https://doi.org/10.1111/cobi.12498

Eads, D. A., and D. E. Biggins. 2019. Plague management of prairie dog colonies: degree and duration of deltamethrin flea control. Journal of Vector Ecology 44:40-47. https://doi.org/10.1111/jvec.12327

Eads, D. A., D. E Biggins, J. Bowser, J. C. McAllister, R. L. Griebel, E. Childers, T. M. Livieri, C. Painter, L. Sterling Krank, and K. Bly. 2018. Resistance to deltamethrin in prairie dog (*Cynomys ludovicianus*) fleas in the field and in the laboratory. Journal of Wildlife Diseases 54:745-754. https://doi.org/10.7589/2017-10-250

Eskey, C. R., and V. H. Haas. 1940. Plague in the western part of the United States. U. S. Public Health Service, Public Health Bulletin 254:1-83.

Forrest, S. C., D. E. Biggins, L. Richardson, T. W. Clark, T. M. Campbell III, K. A. Fagerstone, and E. T. Thorne. 1988. Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981-1985. Journal of Mammalogy 69:261-273. https://doi.org/10.2307/1381377

Gage, K. L. 1999. Plague surveillance. Pages 135-154 in World Health Organization, editor. Plague manual: epidemiology, distribution, surveillance and control. Geneva, Switzerland.

Gage, K. L., and M. Y. Kosoy. 2006. Recent trends in plague ecology. Pages 213-231 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://doi.org/10.3133/sir20055293

Gage, K. L., J. A. Montenieri, and R. E. Thomas. 1994. The role of predators in the ecology, epidemiology, and surveillance of plague in the United States. Pages 200-206 in Proceedings of the 16th Vertebrate Pest Conference. University of Nebraska-Lincoln. https://digitalcommons.unl.edu/vpc16/20/

Godbey, J. L., D. E. Biggins, and D. Garelle. 2006. Exposure of captive black-footed ferrets to plague and implications for species recovery. Pages 233-237 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://doi.org/10.3133/sir20055293

Grogan, L. F., L. Berger, K. Rose, V. Grillo, S. D. Cashins, and L. F. Skerratt. 2014.

Surveillance for emerging biodiversity diseases of wildlife. PLOS Pathogens 10:1-4. https://doi.org/10.1371/journal.ppat.1004015

Haydon, D. T., D. A. Randall, L. Matthews, D. L. Knobel, L. A. Tallents, M. B. Gravenor, S. D. Williams, J. P. Pollinger, S. Cleaveland, M. E. J. Woolhouse, C. Sillero-Zubiri, J. Marino, D. W. Macdonald, and M. K. Laurenson. 2006. Low-coverage vaccination strategies for the conservation of endangered species. Nature 443:692-695. https://doi.org/10.1038/nature05177

Heard, M. J., K. F. Smith, K. J. Ripp, M. Berger, J. Chen, J. Dittmeier, M. Goter, S. T. McGarvey, and E. Ryan. 2013. The threat of disease increases as species move towards extinction. Conservation Biology 27:1378-1388. https://doi.org/10.1111/cobi.12143

Hu, B., S. Han, and H. He. In press. Effect of epidemic diseases on wild animal conservation. Integrative Zoology. https://doi.org/10.1111/1749-4877.12720

Jachowski, D. S., and J. M. Lockhart. 2009. Reintroducing the black-footed ferret *Mustela nigripes* to the Great Plains of North America. Small Carnivore Conservation 41:58-64. https://smallcarnivoreconservation.com/index.php/sccg/issue/view/280/82

Jones, K. E., N. G. Patel, M. A. Levy, A. Storeygard, D. Balk, J. L. Gittleman, and P. Daszak. 2008. Global trends in emerging infectious diseases. Nature 451:990-994. https://doi.org/10.1038/nature06536

Jones, M. E., P. J. Jarman, C. M. Lees, H. Hesterman, R. K. Hamede, N. J. Mooney, D. Mann, C. E. Pukk, J. Bergfeld, and H. McCallum. 2007. Conservation management of Tasmanian devils in the context of an emerging, extinction-threatening disease: devil facial tumor disease. EcoHealth 4:326-337. https://doi.org/10.1007/s10393-007-0120-6

Livieri, T. M., and E. M. Anderson. 2012. Black-footed ferret home ranges in Conata Basin, South Dakota. Western North American Naturalist 72:196-205. https://doi.org/10.3398/064.072.0209

Livieri, T. M., S. C. Forrest, M. R. Matchett, and S. W. Breck. 2022. Conserving endangered black-footed ferrets: biological threats, political challenges, and lessons learned. Pages 458-470 in D. DellaSalla and M. Goldstein, editors. Imperiled: The encyclopedia of conservation. Elsevier. https://doi.org/10.1016/B978-0-12-821139-7.00061-1

Lopez, G., M. Lopez-Parra, L. Fernandez, C. Martinez-Granados, F. Martinez, M. L. Meli, J. M. Gil-Sanchez, N. Viqueira, M. A. Diaz-Portero, R. Cadenas, H. Lutz, A. Vargas, and M. A. Simon. 2009. Management measures to control a feline leukemia virus outbreak in the endangered Iberian lynx. Animal Conservation 12:173-182. https://doi.org/10.1111/j.1469-1795.2009.00241.x

Marinari, P. E., and J. S. Kreeger. 2006. An adaptive management approach for black-footed ferrets in captivity. Pages 23-27 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://doi.org/10.3133/sir20055293

Marino, J., C. Sillero-Zubiri, A. Deressa, E. Bedin, A. Bitewa, F. Lema, G. Rskay, A. Banyard, and A. R. Fooks. 2017. Rabies and distemper outbreaks in smallest Ethiopian wolf population. Emerging Infectious Diseases 23:2102-2104. https://doi.org/10.3201%2Feid2312.170893

Matchett, M. R., D. E. Biggins, V. Carlson, B. Powell and T. Rocke. 2010. Enzootic plague reduces black-footed ferret (*Mustela nigripes*) survival in Montana. Vector-Borne and Zoonotic Diseases 10:27-35. https://doi.org/10.1089/vbz.2009.0053

McCallum, H., and A. Dobson. 1995. Detecting disease and parasite threats to endangered species and ecosystems. Trends in Ecology and Evolution 10:190-194. https://doi.org/10.1016/S0169-5347(00)89050-3

Mize, E. L. 2015. Tracking the spread of emerging sylvatic plague in black-tailed prairie dog metapopulations using a landscape genetics approach. PhD Dissertation, University of South Dakota, Vermillion, SD.

Mize, E. L, and H. B. Britten. 2016. Detections of *Yersinia pestis* east of the known distribution of active plague in the United States. Journal of Vector-Borne and Zoonotic Diseases 16:88-95. https://doi.org/10.1089/vbz.2015.1825

Monterroso, P., G. Garrote, A. Serronha, E. Santos, M. Delibes-Mateos, J. Abrantes, R. Perez de Ayala, F. Silvestre, J. Carvalho, I. Vasco, A. M. Lopes, E. Maio, M. J. Magalhaes, L. S. Mills, P. J. Esteves, M. Angel Simon, and P. C. Alves. 2016. Disease-mediated bottom-up regulation: An emergent virus affects a keystone prey, and alters the dynamics of trophic webs. Scientific Reports 6:1-9. https://doi.org/10.1038/srep36072

Nevison, S. A. 2017. Swift foxes in southwestern South Dakota: assessing the current status of a reintroduced population. MS Thesis, South Dakota State University, Brookings, South Dakota. https://openprairie.sdstate.edu/etd/2152

Preece, N. D., S. E. Abell, L. Grogan, A. Wayne, L. F. Skerratt, P. van Oosterzee, A. L. Shima, P. Daszak, H. Field, A. Reiss, L. Berger, T. L. Rymer, D. O. Fisher, M. J. Lawes, S. G. Laurance, H. McCallum, C. Esson, and J. H. Epstein. 2017. A guide for ecologists: Detecting the role of disease in faunal declines and managing population recovery. Biological Conservation 214:136-146. https://doi.org/10.1016/j.biocon.2017.08.014

Rocke, T. E., S. Smith, P. Marinari, J. Kreeger, J. T. Enama, and B. S. Powell. 2008. Vaccination with F1-V fusion protein protects black-footed ferrets (*Mustela nigripes*) against plague upon oral challenge with *Yersinia pestis*. Journal of Wildlife Diseases 44:1-7. https://doi.org/10.7589/0090-3558-44.1.1

Russell, R. E., G. V. DiRenzo, J. A. Szymanski, K. E. Alger, and E. H. C. Grant. 2020. Principles and mechanisms of wildlife population persistence in the face of disease. Frontiers in Ecology and Evolution 8:569016. https://doi.org/10.3389/fevo.2020.569016

Sandercock, B. K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. Journal of Wildlife Management 70:1504-1520. https://doi.org/10.2193/0022-541X(2006)70[1504:EODPFL]2.0.CO;2

Scheele, B. C., D. A. Hunter, L. F. Grogan, L. Berger, J. E. Kolby, M. S. McFadden, G. Marantelli, L. F. Skerratt, and D. A. Driscoll. 2014. Interventions for reducing risk in Chytridiomycosis-threatened amphibians. Conservation Biology 28:1195-1205. https://doi.org/10.1111/cobi.12322

Schuler, K., M. Claymore, H. Schnitzler, E. Dubovi, T. Rocke, M. J. Perry, D. Bowman, and R. C. Abbott. 2021. Sentinel coyote pathogen survey to assess declining black-footed ferret (*Mustela nigripes*) population in South Dakota, USA. Journal of Wildlife Diseases 57:264-272. https://doi.org/10.7589/JWD-D-20-00015

Scott, M. E. 1988. The impact of infection and disease on animal populations: implications for conservation biology. Conservation Biology 2:40-56. https://doi.org/10.1111/j.1523-1739.1988.tb00334.x

Selakovic, S., P. C. de Ruiter, and H. Heesterbeek. 2014. Infectious disease agents mediate interaction in food webs and ecosystems. Proceedings of the Royal Society B 281:1-10. https://doi.org/10.1098/rspb.2013.2709

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663-688. https://doi.org/10.1093/jmammal/gyw078

Smith, K. F., K. Acevedo-Whitehouse, and A. B. Pedersen. 2009. The role of infectious diseases in biological conservation. Animal Conservation 12:1-12. https://doi.org/10.1111/j.1469-1795.2008.00228.x

Smith, K. F., D. F. Sax, and K. D. Lafferty. 2006. Evidence for the role of infectious disease in species extinction and endangerment. Conservation Biology 20:1349-1357. https://doi.org/10.1111/j.1523-1739.2006.00524.x

Thorne, E. T., and E. S. Williams. 1988. Disease and endangered species: the black-footed ferret as a recent example. Conservation Biology 2:66-74. https://doi.org/10.1111/j.1523-1739.1988.tb00336.x

Thrusfield, M., and R. Christley. 2018. Veterinary Epidemiology. Fourth edition. Wiley, Hoboken, New Jersey. https://onlinelibrary.wiley.com/doi/book/10.1002/9781118280249

Tompkins, D. M., S. Carver, M. E. Jones, M. Krkosek, and L. F. Skerratt. 2015. Emerging infectious diseases of wildlife: a critical perspective. Trends in Parasitology 31:149-159. https://doi.org/10.1016/j.pt.2015.01.007

Tripp, D. W., T. E. Rocke, J. P. Runge, R. C. Abbott, and M. W. Miller. 2017. Burrow dusting or oral vaccination prevents plague-associated prairie dog colony collapse. EcoHealth 14:451-462. https://doi.org/10.1007/s10393-017-1236-y

U.S. Fish and Wildlife Service. 2013. Recovery plan for the black-footed ferret (*Mustela nigripes*). U.S. Fish and Wildlife Service, Denver, Colorado.

https://www.fws.gov/node/68191

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Supplement 46:120-138. https://doi.org/10.1080/00063659909477239

Williams, E. S., J. Edwards, S. Anderson, C. Lynn, V. Welch, W. Edwards, and S. Dubay. 1998. Survey of carnivores for diseases at Conata Basin/Badlands, South Dakota, 1994. Pages 22-31 in G. E. Plumb, G. M. Schroeder, and P. M. McDonald, editors. Black-footed ferret reintroduction in Badlands National Park. National Park Service, Interior, South Dakota.

Williams, E. S., K. Mills, D. R. Kwiatkowski, E. T. Thorne, and A. Boerger-Fields. 1994. Plague in a black-footed ferret (*Mustela nigripes*). Journal of Wildlife Diseases 30:581-585. https://doi.org/10.7589/0090-3558-30.4.581

Williams, E. S., E. T. Thorne, M. J. Appel, and D. W. Belitsky. 1988. Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming. Journal of Wildlife Diseases 24:385-398. https://doi.org/10.7589/0090-3558-24.3.385

Williams, E. S., E. T. Thorne, T. J. Quan, and S. L. Anderson. 1991. Experimental infection of domestic ferrets (*Mustela putorius furo*) and Siberian polecats (*Mustela eversmanni*) with *Yersinia pestis*. Journal of Wildlife Diseases 27:441-445. https://doi.org/10.7589/0090-3558-27.3.441

Wimsatt, J., D. E. Biggins, E. S. Williams, and V. M. Becerra. 2006. The quest for a safe and effective canine distemper virus vaccine for black-footed ferrets. Pages 248-266 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://pubs.usgs.gov/publication/70180915

Wisely, S. M. 2019. Wildlife disease management in the global context. Pages 94-111 in J. L. Koprowski and P. R. Krausman, editors. International wildlife management: conservation challenges in a changing world. Johns Hopkins University Press, Baltimore, Maryland. https://doi.org/10.1353/book.67482

Woodroffe, R. 1999. Managing disease threats to wild mammals. Animal Conservation 2:185-193. https://doi.org/10.1111/j.1469-1795.1999.tb00064.x

Wright, M. L., T. M. Livieri, and R. M. Santymire. 2022. Recombitek canine distemper vaccine as an alternative for Purevax distemper vaccine in endangered black-footed ferrets (*Mustela nigripes*). Journal of Zoo and Wildlife Medicine 53:194-199. https://doi.org/10.1638/2020-0228

3. DISEASE SHIFTS DIET OF AN ENDANGERED SPECIALIST CARNIVORE: BLACK-FOOTED FERRETS, PRAIRIE DOGS, AND PLAGUE

Summary

Diseases can induce strong direct and indirect effects on wildlife populations. In North America, invasive plague (caused by *Yersinia pestis*) results in high mortality of endangered black-footed ferrets (*Mustela nigripes*) and their primary prey, prairie dogs (*Cynomys* spp.), as well as altering the abundance of secondary small mammal prey resources. To explore the effect of plague on black-footed ferret diet and foraging, we used stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope compositions of mammalian hair to estimate assimilated diets of wild ferrets in South Dakota prior to (1998-2007) and during (2008-2015) a plague epizootic. We also investigated the effects of plague mitigation through deltamethrin dusting of burrows for flea vector control on black-footed ferret diets. We captured and measured isotopes of 859 black-footed ferrets, 26 black-tailed prairie dogs (*C. ludovicianus*), and 19 deer mice (*Peromyscus sonoriensis*), which are the most abundant alternative prey item for ferrets in our study area. Prior to the invasion of plague and deltamethrin dust application, the diets of black-footed ferrets were predominantly composed of prairie dogs (67%) but this increased to 94% following the invasion of plague and to 99% on colonies that received deltamethrin dust to manage plague. Thus, plague and application of deltamethrin dust to protect ferrets and prairie dogs likely reduced deer mouse populations, limiting their availability as alternative prey to black-footed ferrets. Prior to plague invasion, deer mice, the most abundant small rodent on the prairie dog study colonies, comprised nearly one third of the black-footed ferret diet, which may be typical of historical prey preferences of ferret populations. Despite observed foraging plasticity, black-

footed ferrets can be considered prairie dog colony specialists and any diet effects following deltamethrin dust treatment are likely less severe than the impacts of plague on unprotected ferret populations.

Introduction

Disease can have pronounced direct and indirect effects on wildlife populations (Tompkins et al. 2011). Direct effects include mortality and reduced fecundity leading to lower fitness (Smith et al. 2009). Indirect impacts can be more difficult to observe but may alter predator-prey dynamics and community composition or induce trophic cascades (Buck and Ripple 2017). For instance, an outbreak of mange reduced populations of Andean vicuñas (*Vicugna vicugna*), restructuring the trophic interactions with a predator (puma, *Puma concolor*) and scavenger (Andean condor, *Vultur gryphus*), thereby increasing plant biomass and altering the ecosystem (Monk et al. 2022). The indirect effects of disease can further imperil endangered species, particularly those that are specialists or rely on resources provided by typically abundant species. In Spain, a hemorrhagic virus reduced populations of European rabbits (*Oryctolagus cuniculus*), which negatively impacted two endangered predators, Iberian lynx (*Lynx pardinus*) and Spanish Imperial eagles (*Aquila adalberti*; Monterroso et al. 2016).

In North America, the bacterium *Yersinia pestis* causes sylvatic plague in prairie dogs (*Cynomys* spp.), with >90% mortality observed during epizootics (Antolin et al. 2002, Pauli et al. 2006, Biggins et al. 2021). Black-footed ferrets (*Mustela nigripes*) are highly specialized predators of prairie dogs and utilize their burrows and colonies as habitat (Biggins et al. 2006a). In addition to reducing prairie dog abundance on colonies, plague outbreaks directly affect black-footed ferrets as they are susceptible to plague at even low exposure levels and experience high mortality rates when infected (Godbey et al. 2006, Rocke et al. 2004, 2008). Plague can persist in prairie dog colonies at low, enzootic levels while affecting survival of both prairie dogs (Biggins et al. 2010) and black-footed ferrets (Matchett et al. 2010), and likely other small mammals. Additionally, other rodents associated with prairie dog colonies appear to serve as hosts or amplifiers of plague with varying disease susceptibility (Abbott and Rocke 2012). Deer mice (*Peromyscus sonoriensis*) are a common small mammal on prairie dog colonies that exhibit variable survival rates in response to plague epizootics (Gage and Kosoy 2005) with documented reductions in survival of 40-60% or more due to plague (Bron et al. 2021, Goldberg et al. 2022b). Thus, plague has the potential to not only cause direct mortality of black-footed ferrets and reduce their primary prey but also appears to significantly affect small mammal abundance overall (Eads and Biggins 2015).

Plague is transmitted by fleas, and the disease is often mitigated for both prairie dogs and black-footed ferrets through the application of 0.05% deltamethrin dust (DeltaDust®, Bayer Environmental Science, Research Triangle Park, NC) into prairie dog burrows (Biggins et al. 2021, Matchett et al. 2010, Tripp et al. 2017). Dusting may prevent a prairie dog colony from collapsing during a plague epizootic, thereby maintaining the prairie dog food source and burrow systems for black-footed ferrets, but dusting may also negatively affect short-term survival of some small mammals through direct toxicity or reduction in arthropod prey, although high reproductive rates and variable survival rates among species and locations may ameliorate this effect (Dombro 2016, Goldberg et al. 2022a). While the diet of black-footed ferrets consists mostly of prairie dogs, predation on other species, including birds, mice, and other small mammals, has been observed in the wild (Henderson et al. 1969, Eads 2012). Black-footed ferret scats collected from black-tailed prairie dog (*C. ludovicianus*) burrows in South Dakota contained prairie dog remains in 91% of scats and mice in 26% of scats (Sheets et al. 1972), whereas ferret scats from white-tailed prairie dog (*C. leucurus*) colonies near Meeteetse, Wyoming, had prairie dogs in 87%, mice in 6%, and lagomorphs in 3% of scats (Campbell et al. 1987).

Based on stable isotope composition of black-footed ferret hair samples collected from a white-tailed prairie dog complex in Shirley Basin, Wyoming, Brickner et al. (2014) found that during the summer, adult male and juvenile ferrets consumed mostly white-tailed prairie dogs (~75% of their diet) with the remaining portion of the diet filled by mice and mid-sized mammals. However, the diet of adult female black-footed ferrets was lower in prairie dogs (63% of their diet) and higher in other mammals, supporting the hypothesis that there is greater foraging plasticity than typically assumed for this specialized predator (Campbell et al. 1987). White-tailed prairie dogs typically occupy colonies at a lower density of individuals compared to black-tailed prairie dogs, which may force ferrets to consume alternative prey to meet their dietary needs (Brickner et al. 2014). To what degree black-footed ferrets that occupy higher density black-tailed prairie dog colonies demonstrate foraging plasticity is unknown. Further, the effects of plague and plague management (dusting) on black-footed ferret diets are unknown. Indeed, plague may shift black-footed ferrets towards more of a generalist diet (fewer prairie dogs, more small mammals) or a specialist diet (more prairie dogs, fewer small mammals) depending upon how plague affects prey availability, while dusting may increase prairie dog survival and availability when plague is present but reduce short-term small mammal availability.

The goal of our study was to generate stable isotope-based quantitative estimates of black-footed ferret diet composition on black-tailed prairie dog colonies in relation to a plague epizootic and plague management (dusting). Specifically, we predicted the invasion of epizootic plague would shift black-footed ferret isotopic diet compositions to include fewer prairie dogs because increased mortality of annual-breeding prairie dogs (Hoogland 1996) would decrease their availability as prey, but a higher reproductive rate in mice and other small mammals (Goldberg et al. 2022b) may maintain their relative availability to ferrets, compared with prairie dogs. Next, we predicted that dusting prairie dog burrows during the plague period would reduce mortality in prairie dogs, thereby increasing prairie dogs in black-footed ferret diets relative to small mammals, which may have higher mortality and reduced availability because of both plague and dusting combined. Lastly, we predicted that assimilated diet composition of black-footed ferrets occupying high density black-tailed prairie dog colonies would contain a higher proportion of prairie dogs than those reported for lower density white-tailed prairie dogs (Brickner et al. 2014).

Methods

Study area

Our study area was ~92,000 ha of the Conata Basin, a portion of the Buffalo Gap National Grassland, and the adjacent Badlands National Park (CB/BADL hereafter) in southwestern South Dakota. Black-footed ferrets were reintroduced to prairie dog colonies in CB/BADL during 1994-1999, resulting in a free-ranging population. The area contained 4,100 – 14,100 ha of black-tailed prairie dog colonies from 1998-2015. Vegetation of this mixed-grass prairie is dominated by western wheatgrass (*Pascopyron smithii*), buffalograss (*Bouteloa dactyloides*), and blue grama (*Bouteloua gracilis*).

Animal sampling

We sampled black-footed ferrets from 1998-2015 during annual population monitoring activities (Black-Footed Ferret Recovery Implementation Team 2016) under United States Fish and Wildlife Service permit #TE064682-1 and followed the guidelines of Sikes et al. (2016) for handling of ferrets, prairie dogs, and small mammals. We collected 1-3 tufts of hair from the dorsal surface of anesthetized black-footed ferrets using forceps to quickly remove the full hair to the root. Black-footed ferrets molt their pelage bi-annually, and we assumed our sampling represented the summer pelage grown since the spring molt. We marked black-footed ferrets with passive integrated transponder (PIT) tags (AVID Friendchip 125 kHz, Norco, CA) and classified them as adults or juveniles based upon canine tooth characteristics (Santymire et al. 2012). We collected samples from black-footed ferrets in three prairie dog colony sub-complexes (Agate, Heck Table, and Sage Creek; Phillips et al. 2020) to maintain spatial replication across the pre-plague and plague periods.

We opportunistically collected hair in 2014 from black-tailed prairie dogs and other small mammals during live-trapping for other studies (Eads et al. 2018, Goldberg et al. 2022a). We captured prairie dogs using Tomahawk live traps (Tomahawk Live Trap, Hazelhurst, WI) and anesthetized them with isoflurane for flea combing, during which we plucked one tuft of hair from the dorsal surface using forceps. We captured small mammals using Sherman traps (HB Sherman Inc., Tallahassee, FL), transferred them to a small plastic bag for handling, and plucked one tuft of hair from the dorsal surface using forceps. We trapped, handled, sampled, and released all prairie dogs and small rodents following the U. S. Geological Survey Institutional Animal Care and Use Committee protocol 2015-07 (Eads et al. 2018).

Plague was confirmed on our study site for the first time in 2008 (Rocke et al. 2008, Chapter 2); thus, black-footed ferret samples from 1998-2007 are considered the pre-plague period and from 2008-2015 as the plague period. Dusting of prairie dog burrows for flea vector control occurred annually during summer-fall on select colonies beginning in 2005, during the pre-plague period as prophylaxis, then during the plague period as a mitigation measure, and continued for the duration of our study. Dusted colonies were subsequently dusted again annually. Because dusting and black-footed ferret sampling often overlapped temporally (Chapter 2), any potential dusting effects on availability of prairie dogs and small mammals would not be reflected in the summer pelage. Thus, we classified a black-footed ferret sample as occupying a dusted prairie dog colony only if dusting occurred in the previous season, potentially affecting prey availability over the fall-winter-spring, which would then be reflected in the next summer pelage. For instance, a black-footed ferret sampled in September 2010 on a colony dusted the previous year (2009) would be considered as dusted. However, if that colony was only dusted for the first time in the same season of capture (2010), then the black-footed ferret sample would be considered non-dusted.

We stored hair samples dry in coin envelopes (5.7 x 8.9 cm) and kept them frozen until lab analysis. Hair was washed three times in 2:1 mixture of chloroform:methanol and allowed to air dry at room temperature. Approximately 1 mg of hair was massed into tin capsules (4 x 6 mm; Costech Analytical, Inc.) for stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope analyses using an elemental analyzer (Carlo Erba NC2500) interfaced to a mass spectrometer (Micromass Optima) at the USGS Stable Isotope Laboratory in Denver, Colorado.

Data analyses

In addition to prairie dogs, we identified and sampled multiple small mammal species in our study area that may also be prey for black-footed ferrets, including cottontail rabbits (*Sylvilagus* spp.), northern grasshopper mice (*Onchomys leucogaster*), deer mice, hispid pocket mice (*Chaetodipus hispidus*), and voles (*Microtus* spp.). We retained two isotopically distinct and meaningful dietary sources for analysis, prairie dogs and deer mice, for several reasons: 1) deer mice are consistently the most abundant small mammal on prairie dog colonies in our study area with over twice the abundance of grasshopper mice, while hispid pocket mice and voles had low abundance or were altogether absent (Agnew et al. 1986, Cully et al. 2010, Bron et al. 2019); 2) previous research in our study area detected high variation in cottontail abundance on prairie dog colonies (Eads et al. 2015, Windell et al. in review) and our isotopic data for cottontails overlapped with prairie dogs (MANCOVA; $F_{2,29} = 1.77$, $p = 0.19$; Table 3.1) making them indistinguishable; and 3) our grasshopper mice isotopic estimates were less robust than deer mice because of small sample size ($n = 2$; Table 3.1). Our reduction of dietary sources to only prairie dog and deer mouse may have missed rare prey items and potentially caused some bias in our dietary estimates (Phillips et al. 2014). However, our primary interest was observing any potential shift in the proportion of prairie dogs in black-footed ferret diets relative to demography, disease, and disease management rather than accurately estimating proportions of all assimilated prey species. Thus, we considered deer mice as a representative alternative prey source to prairie dogs.

We estimated the proportional assimilation of prairie dogs and deer mice by black-footed ferrets using a Bayesian-based mixing model in MixSIAR (Stock et al. 2018) with Markov chain Monte Carlo (MCMC; chain length = 300,000; burn = 200,000; thin = 100; chains = 3). We used raw isotopic composition values (i.e., in lieu of point estimates) of the prey and the trophic discrimination factors of 3.8‰ ± 0.03 for $\delta^{15}N$, based on a species-specific controlled trial for black-footed ferrets from diet to hair (Brickner et al. 2014), that were corrected with a muscle-hair isotopic offset of 2.1‰ ± 0.1‰ for $\delta^{13}C$ for carnivores (Stephens et al. 2022). We ran MixSIAR model sets with a factorial analysis using age-sex class (adult males, adult females and juveniles) and period (pre-plague and plague) as fixed effects and using a hierarchical analysis with treatment (dust, no dust) nested within period. For both analyses we used an uninformed (i.e., generalist) prior and an informed prior based on previous reports of black-footed ferret diet proportions (90% prairie dogs and 10% deer mice; Sheets et al. 1972, Campbell et al. 1987). We reported the median and 95% credibility interval (95% CI) to summarize the isotopic mixing space and the posterior diet distribution calculated by all models.

Results

We sampled 851 individual black-footed ferrets for a total of 859 samples with 613 samples from the pre-plague period and 246 samples during plague (Table 3.2). Within the plague period, we sampled seven individuals more than once with six individuals in two different years and one individual in three different years. Sampling occurred between 16 August and 31 October from 1998-2015, although no samples were collected in 2003. During the pre-plague period, we collected 37 samples in August, 292 in September, and 284 in October. During plague, we collected 49 samples in August, 122 in September, and 75 in October. We collected prey samples only in 2014 (23 July-21 October), including grasshopper mice and cottontail rabbits, but retained only prairie dogs and deer mice, which were isotopically distinct (MANOVA; $F_{2,42} = 80.5$, $p < 0.001$; Table 3.1), for modeling.

Black-footed ferret isotopic compositions were dispersed throughout the isotopic mixing space, suggesting possible dietary diversity (Figure 3.1). The adult female bivariate mean values substantially overlapped with all age-sex classes during both pre-plague and plague time periods. However, mean values for adult males were distinct from juveniles without any overlap during both time periods. We observed a shift towards prairie dogs in bivariate mean values for each age-sex class from pre-plague to plague time periods (Figure 3.1). Likewise, our mixing models suggested a notable shift in the proportion of prairie dog in black-footed ferret diet with the invasion of plague (Figure 3.2; Gelman-Rubin diagnostic: Out of 869 variables: 3 > 1.01 and 0 > 1.05). In areas not treated with dust, the proportion of prairie dog in black-footed ferret diet increased from a median of 67% (95% CI = 58 - 74%) to 94% (95% CI = 88 – 99%) with the invasion of plague (Table 3.3). Considering dusted prairie dog colonies and using informed priors, the proportion of prairie dogs in black-footed ferret diets had a median of 98% (95% CI = 92 – 100%) prior to plague and then 99% (95% CI = 99 – 100%) during plague (Table 3.3). The estimated diet was similar across age-sex classes of black-footed ferrets with a slightly higher abundance of prairie dogs in the diet of adult males compared to adult females and juveniles during the pre-plague period using both informed and uninformed priors (Table 3.4).

Discussion

Plague can cause high mortality rates in endangered black-footed ferrets and their prairie dog prey base (Eads and Biggins 2015); thus, management of this disease is a high priority for ferret conservation (U.S. Fish and Wildlife Service 2019). Our study sought to understand if plague may alter the proportion of prairie dogs in black-footed ferret diets, and if plague mitigation (dusting), would ameliorate any potential effects on diet. Median estimates of prairie dog proportions in all black-footed ferret diets shifted from 67% to 94% prairie dogs with the invasion of plague into non-dusted prairie dog colonies, suggestive of a disease-mediated diet shift, coinciding with the first known invasion of epizootic plague into our study area that caused dramatic declines in prairie dog and ferret populations from 2008-2015 (Chapter 2). On dusted prairie dog colonies, we observed a similar human-mediated shift of prairie dog proportions in black-footed ferret diets from 67% to 98% prior to plague and the combination of plague and dusting further shifted ferret diets to 99% prairie dogs. Our prediction of a disease-mediated diet shift was supported, but resulting in a higher proportion of prairie dogs, which was opposite of what we anticipated.

We sampled 57 black-footed ferrets on non-dusted colonies during plague without any visual effects of disease (e.g., inactive burrows, reduced prairie dog activity) in those areas, although epizootic plague was visually observed on nearby (0.5 – 20.4 km) colonies. Interestingly, these sampled black-footed ferrets were not vaccinated against plague (Matchett et al. 2010, Chapter 2) and several potential factors may explain why ferrets shifted their diets towards prairie dogs prior to those colonies being dusted or visually affected by plague. First, the bacterial disease tularemia (*Francisella tularensis*) may have caused die-offs of deer mice (Wobeser et al. 2007) and other small mammals on prairie dog colonies with prairie dogs and black-footed ferrets relatively unaffected (Cherry et al. 2019, Matchett et al. 2021). Second, the invasion of epizootic plague into CB/BADL may have occurred concurrently with, or possibly after, an enzootic level of plague infection among deer mice and their fleas without affecting prairie dog and black-footed ferret survival. Deer mice are a primary host for *Aetheca wagneri* (Salkeld and Stapp 2008, Thiagarajan et al. 2008, Russell et al. 2018), a flea species that can be infected with plague (Cully and Williams 2001, Bron et al. 2019). This flea species may not be involved in epizootic transmission (Eisen et al. 2008), but could assist in plague maintenance among deer mice on non-dusted prairie dog colonies lacking evidence of epizootic plague (Eads et al. 2020, Colman et al. 2021). *Aetheca wagneri* is rarely found on black-tailed prairie dogs (Cully and Williams 2001) or black-footed ferrets (Harris et al. 2014). It is conceivable that plague-infected *A. wagneri* caused a decline of deer mouse populations on non-dusted colonies and surviving black-footed ferrets responded by shifting their diet towards prairie dogs. Black-footed ferrets are very susceptible to plague (Godbey et al. 2006), but a study of enzootic plague in Montana found that some can survive temporarily (0.23 six-month re-encounter rate) without dusting or vaccination in prairie dog colonies affected by enzootic plague (Matchett et al. 2010).

Supporting our predictions, it appeared that dusting prairie dog burrows reduced the availability of alternative prey, similar to the effect of plague, and black-footed ferrets responded by assimilating more prairie dogs, and thus less deer mice, in their diet. Previous studies in South Dakota found that deltamethrin dust had no noticeable effect on deer mouse survival on prairie dog colonies (Maestas and Britten 2019) but suggested that repeated application of dust could reduce arthropod populations that deer mice depend upon (Dombro 2016). Large prairie dog colonies in our study area were targeted for repeated annual dust application to provide some protection to black-footed ferrets and their prey base (Chapter 2), but those actions may have inadvertently altered arthropod and thus deer mouse populations. More recently, Goldberg et al. (2022a) found that deltamethrin dust reduced monthly survival of deer mice and other small rodents, possibly through direct toxicity (in contrast to the findings of Dombro 2016), although high fecundity in mice populations (Brown 1966, Millar 1985) may ameliorate any negative effects of deltamethrin dust over longer periods. Although we observed a difference in black-footed ferret diets related to dusting, deltamethrin is an effective tool for reducing fleas for conservation of prairie dogs and black-footed ferrets (Biggins et al. 2010, 2021, Matchett et al.

2010, Chapter 2) and the net benefits of potential plague mitigation likely outweigh any consequences of changes in alternative prey.

The black-footed ferret population at CB/BADL was established with the reintroduction of captive animals from 1994-1999 and subsequently became the largest wild population with a minimum of 355 individuals estimated in 2007, prior to the invasion of plague (Chapter 2). During this pre-plague period (1998-2007), the black-footed ferret population at CB/BADL likely functioned similarly to historical pre-1900 populations in the region because it was self-sustaining, and the prairie dog habitat was mostly pristine without invasive plague. Thus, the 67% proportion of prairie dog that we estimated in pre-plague black-footed ferret diets may be similar to historic ferret diets on these habitats. This estimate is also comparable to the proportion of white-tailed prairie dog found in the diet of Wyoming black-footed ferrets (~70%; Brickner et al. 2014), despite differences in prairie dog density and contrary to our predictions. In CB/BADL, active black-tailed prairie dog burrow densities were 158.3/ha (Livieri 2007) compared to 69.2 - 116.1/ha observed for white-tailed prairie dogs in Wyoming (Baker et al. 1999, Biggins et al. 1999), but both areas have prairie dog densities sufficient to support black-footed ferret populations (Biggins et al. 2006b) and both species may be similarly nourishing for ferrets (Dierenfeld et al. 2021).

The foraging plasticity of black-footed ferrets observed here and elsewhere (Brickner et al. 2014), as well as discovered fossil specimens of ferrets outside the range of prairie dogs, has led to postulation that reintroduced ferrets could occupy a broader range of habitats beyond prairie dog colonies (Owen et al. 2000) and that ferrets may not be strictly prairie dog specialists (Fox et al. 2017). Our results suggest approximately one-third of the assimilated diet of black-footed ferrets could be prey species other than prairie dogs; thus, we posit that ferrets are prairie dog colony specialists rather than dietary specialists. Prairie dog colonies and the extensive burrow systems created by prairie dogs, which black-footed ferrets prefer over tunnels created by other animals (Biggins et al. 2006a), provide resources for all aspects of the ferret life history, including refuge, reproduction, and high-density prey populations. The earliest naturalist accounts of black-footed ferrets, prior to widespread prairie dog poisoning campaigns and the accidental introduction of plague that initiated the rapid decline of ferrets, described ferret specimens as associated with prairie dogs (Coues 1877). Lakota indigenous knowledge described the black-footed ferret as a "black-faced prairie dog" and closely associated it with prairie dogs (Cahalane 1954, Henderson et al. 1969). Based upon continued contemporary black-footed ferret preference for prairie dog colonies and early species descriptions prior to the widespread decline of the species, we contend that, while ferrets will consume a variety of prey species, they are dependent on prairie dogs for the prey they provide, habitat they create, and secondary prey species they facilitate.

Our estimates of black-footed ferret diet proportions have several limitations: 1) we restricted our models to only prairie dog and deer mouse as prey items; 2) we sampled prey during only one year in limited portions of our study area; and 3) our ferret hair sampling and dusting priorities led to an unbalanced design with fewer adults sampled. While prairie dogs are the known primary prey for black-footed ferrets, the true role of abundant deer mice in ferret diets is less understood and, in our models, served to represent an alternative prey source to prairie dogs. While it is possible that cottontail rabbits comprise some portion of the black-footed ferret diet, our rabbit samples ($n = 6$) were isotopically equivalent to prairie dogs, possibly because they are forage competitors (Eads et al. 2016); thus, additional isotopes or scat analysis may be needed for estimation. Visual inspection of the bi-variate data plot (Figure 3.1) suggests there may be a prey item in the lower right that was not sampled by our study. We did not sample 13-lined ground squirrels (*Ictidomys tridecemlineatus*), which are present in our study area at low abundances, or birds that utilize prairie dog colonies and may be prey for black-footed ferrets (Eads 2012, Tretten 2019). Next, our prey sampling only occurred in 2014 during the plague period and did not include any samples from the pre-plague period that would further support our black-footed ferret diet shift observations.

The demographic consequence of a disease-mediated diet shift towards more prairie dogs for the black-footed ferrets at CB/BADL is not fully understood. Nonetheless, the ferret population persisted through a plague epizootic, due to extensive plague management efforts (i.e., dusting and vaccination; Chapter 2). As researchers continue to identify other potential plague mitigation tools (Eads et al. 2019, 2021, Matchett et al. 2023), possible effects on deer mice and other alternative prey are being considered and measured (Eads et al. 2022). However, the effects of a human-mediated diet change on black-footed ferrets, through plague management, are likely to be less severe than the devastating effects of plague on unprotected ferrets and prairie dogs.

Contributors

Coauthors on the anticipated publication from this chapter include Dean E. Biggins, David A. Eads, Craig A. Stricker, Gonzalo F. Barceló, and Jonathan N. Pauli. We thank E. Marchini and J. Bowser for assistance with prey sample collection and lab work. P. Cryan and P. Stevens at USGS – Fort Collins Science Center facilitated and supported lab work. S. Wisely and B. Swanson generously stored and shared samples. D. Sargent, B. Perry, and B. Kenner provided field support. We thank L. Angeloni, M. Antolin, and K. Crooks for critical reviews of the manuscript. This research was supported by Prairie Wildlife Research, US Forest Service – Wall Ranger District, Badlands National Park, USGS Fort Collins Science Center, and Badlands Natural History Association. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Table 3.1: Mean isotopic values (95% confidence interval) of potential prey items for black-footed ferrets at Conata Basin/Badlands National Park, South Dakota.

Species	n	$\delta^{13}C$	$\delta^{15}N$
Black-tailed prairie dog (*Cynomys ludovicianus*)	26	-24.2 (0.3)	2.4 (0.2)
Cottontail rabbit (*Sylvilagus* spp.)	6	-23.2 (0.6)	2.0 (0.6)
Deer mouse (*Peromyscus sonoriensis*)	19	-17.3 (0.5)	4.2 (0.2)
Grasshopper mouse (*Onchomys leucogaster*)	2	-21.4 (0.1)	6.7 (0.1)

Table 3.2: Black-footed ferret hair samples prepared and analyzed for stable isotope analyses in Conata Basin/Badlands National Park, South Dakota.

Treatment	Period	Adult Female	Adult Male	Juvenile	Total
Dust	Pre-plague	0	2	21	23
	Plague	20	12	157	189
No dust	Pre-plague	25	25	540	590
	Plague	24	0	33	57
Total		69	39	751	859

Table 3.3: Proportion of prairie dog in assimilated diet of black-footed ferrets occupying dust-treated and non-treated prairie dog colonies prior to the invasion of plague (1998-2007) and during plague (2008-2015) based on isotopic Bayesian mixing models (median ± 95% credible intervals) using informed and uninformed priors.

Period (priors)	Dusted	Non-dusted
Pre-plague (informed)	98% (92 – 100)	67% (58 – 74)
Plague (informed)	99% (99 – 100)	94% (88 – 99)
Pre-plague (uninformed)	96% (90 – 99)	67% (58 – 74)
Plague (uninformed)	99% (98 – 100)	93% (87 – 98)

Table 3.4: Proportion of prairie dog in assimilated diet of black-footed ferrets by age-sex class in Conata Basin/Badlands National Park, South Dakota, pre-plague (1998 – 2007) and during plague (2008 – 2015) based on isotopic Bayesian mixing models (median ± 95% credible intervals). Estimates were made using an informed and uninformed prior.

Period (priors)	Adult males	Adult females	Juveniles
Pre-plague (informed)	73% (63 – 83)	66% (53 – 76)	62% (52 – 70)
Plague (informed)	98% (92 – 100)	97% (90 – 99)	96% (89 – 99)
Pre-plague (uninformed)	72% (60 – 82)	65% (52 – 75)	61% (52 – 69)
Plague (uninformed)	97% (91 – 99)	95% (88 – 99)	94% (88 – 98)

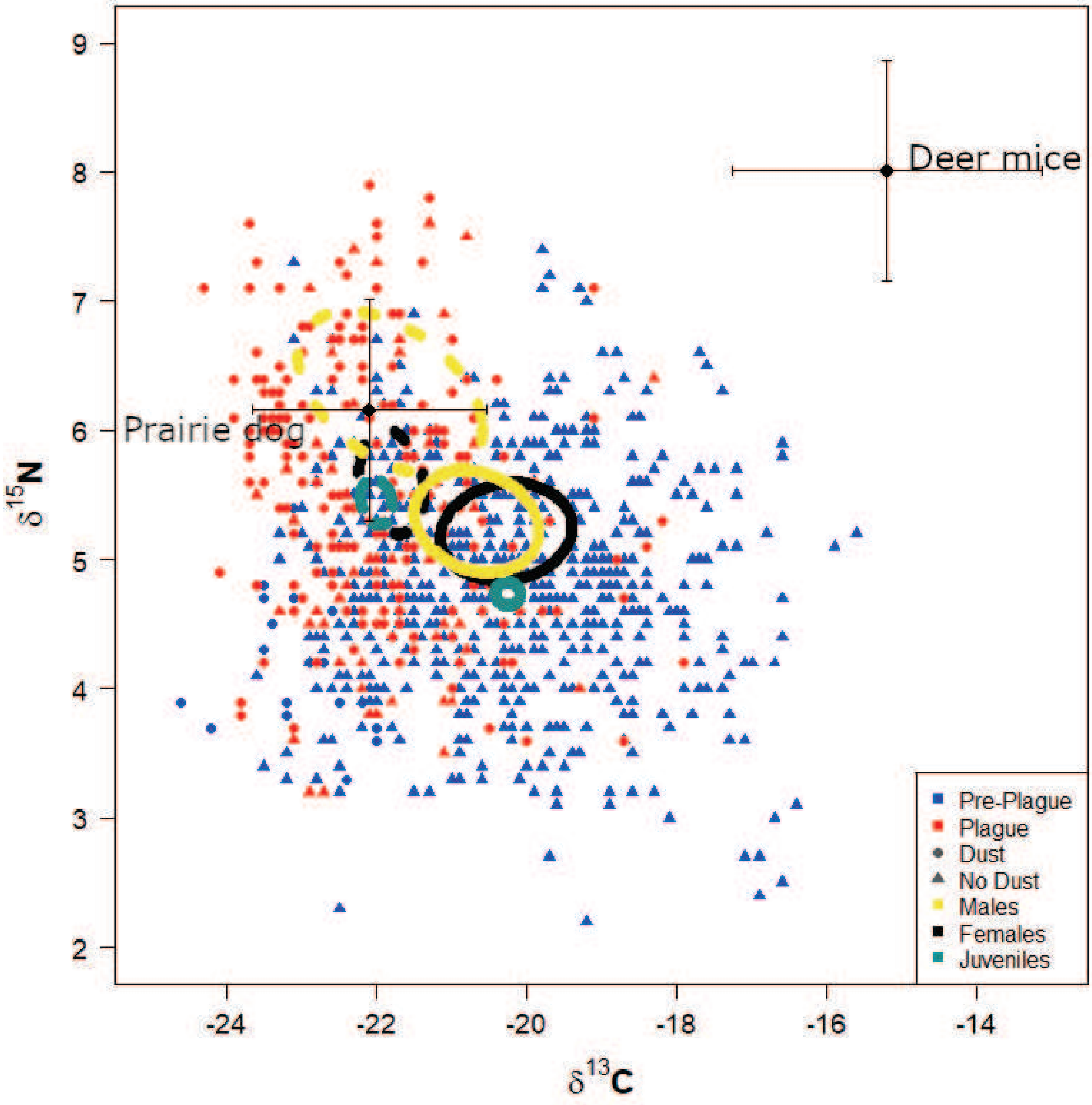

Figure 3.1: Stable isotope compositions ($\delta^{13}C$ and $\delta^{15}N$) of black-footed ferrets; pre-plague (blue) and during plague (red) occupying dusted (circle) or non-dusted (triangles) prairie dog colonies. Ellipses show the 95% confidence interval around bivariate means for adult males (yellow), adult females (black) and juveniles (green) ferrets pre-plague (continuous line) and during plague (dashed line). Also shown are the primary prey items, prairie dogs and deer mice, in our study area (mean ± SD, corrected by trophic discrimination factor).

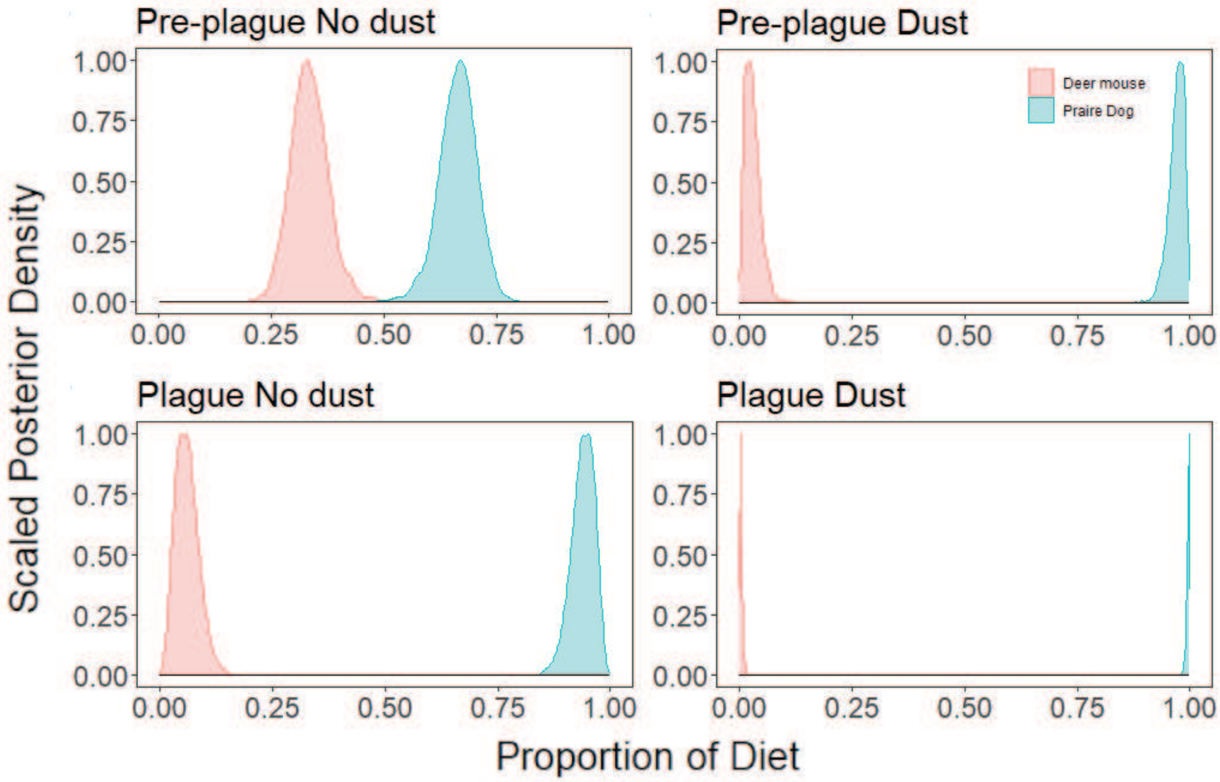

Figure 3.2: Proportion of deer mice (red) and prairie dog (blue) in the assimilated diet of black-footed ferrets occupying dust-treated and non-treated prairie dog colonies during pre-plague (1998 – 2007) and plague (2008 – 2015) periods at Conata Basin/Badlands National Park, South Dakota. Estimates are from a hierarchal Bayesian mixing model based on the informed prior.

REFERENCES

Abbott, R. C., and T. E. Rocke. 2012. Plague. United States Geological Survey Circular 1372. 79p. https://pubs.usgs.gov/circ/1372/

Agnew, W., D. W. Uresk, and R. M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. Journal of Range Management 39:135-139. https://doi.org/10.2307/3899285

Antolin, M. F., P. Gober, B. Luce, D. E. Biggins, W. E. Van Pelt, D. B. Seery, M. Lockhart, and M. Ball. 2002. The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. Transactions of the 67th North American Wildlife and Natural Resources Conference 67:104-127. https://digitalcommons.unl.edu/usfwspubs/57/

Baker, B. W., T. R. Stanley, and J. A. Sedgwick. 1999. Predation of artificial ground nests on white-tailed prairie dog colonies. Journal of Wildlife Management 63:270-277. https://doi.org/10.2307/3802509

Biggins, D. E., J. L. Godey, and D. A. Eads. 2021. Epizootic plague in prairie dogs: correlates and control with deltamethrin. Vector-Borne and Zoonotic Diseases 21:172-178. https://doi.org/10.1089/vbz.2020.2684

Biggins, D. E., J. L. Godbey, K. L. Gage, L. G. Carter, and J. A. Montenieri. 2010. Vector control improves survival of prairie dogs (*Cynomys*) in areas considered enzootic for plague. Vector-Borne and Zoonotic Diseases 10:17-26. https://doi.org/10.1089/vbz.2009.0049

Biggins, D. E., J. L. Godbey, M. R. Matchett and T. M. Livieri. 2006a. Habitat preferences and intraspecific competition in black-footed ferrets. Pages 129-140 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://pubs.usgs.gov/publication/70180909

Biggins, D. E., J. M. Lockhart, and J. L. Godbey. 2006b. Evaluating habitat for black-footed ferrets: revision of an existing model. Pages 143-150 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://pubs.usgs.gov/publication/70180908

Biggins, D. E., A. Vargas, J. L. Godbey, and S. H. Anderson. 1999. Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*). Biological Conservation 89:121-129. https://doi.org/10.1016/S0006-3207(98)00158-X

Black-Footed Ferret Recovery Implementation Team. 2016. Black-footed ferret field operations manual. U. S. Fish and Wildlife Service, Wellington, Colorado. https://www.fws.gov/sites/default/files/documents/black-footed-ferret-field-operations-manual-2016.pdf

Brickner, K. M., M. B. Grenier, A. E. Crosier, and J. N. Pauli. 2014. Foraging plasticity in a highly specialized carnivore, the endangered black-footed ferret. Biological Conservation 169:1-5. https://doi.org/10.1016/j.biocon.2013.10.010

Bron, G. M., C. M. Malave, J. T. Boulerice, J. E. Osorio, and T. E. Rocke. 2019. Plague-positive mouse fleas on mice before plague induced die-offs in black-tailed and white-tailed prairie dogs. Vector Borne and Zoonotic Diseases 19:486-493. https://doi.org/10.1089/vbz.2018.2322

Bron, G. M., S. R. Smith, J. D. Williamson, D. W. Tripp, and T. E. Rocke. 2021. Moderate susceptibility to subcutaneous plague (*Yersinia pestis*) challenge in vaccine-treated and untreated Sonoran deer mice (*Peromyscus maniculatus sonoriensis*) and northern grasshopper mice (*Onychomys leucogaster*). Journal of Wildlife Diseases 57:632-636. https://doi.org/10.7589/JWD-D-20-00122

Brown, L. N. 1966. Reproduction of *Peromyscus maniculatus* in the Laramie Basin of Wyoming. American Midland Naturalist 76:183-189. https://doi.org/10.2307/2423241

Buck, J. C., and W. J. Ripple. 2017. Infectious agents trigger trophic cascades. Trends in Ecology and Evolution 32:681-694. https://doi.org/10.1016/j.tree.2017.06.009

Cahalane, V. H. 1954. Status of the black-footed ferret. Journal of Mammalogy 35:418-424. https://doi.org/10.2307/1375967

Campbell III, T. M., T. W. Clark, L. Richardson, S. C. Forrest, and B. R. Houston. 1987. Food habits of Wyoming black-footed ferrets. American Midland Naturalist 117:208-210. https://doi.org/10.2307/2425722

Cherry, C. C., N. A. Kwit, R. E. Ohms, A. M. Hammesfahr, R. Pappert. J. M. Petersen, C. A. Nelson, and D. E. Buttke. 2019. Tularemia (*Francisella tularensis*) in a black-tailed prairie dog (*Cynomys ludovicianus*) colony. Journal of Wildlife Diseases 55:944-946. https://doi.org/10.7589/2018-05-133

Colman, R. E., R. J. Brinkerhoff, J. D. Busch, C. Ray, A. Doyle, J. W. Sahl, P. Keim, S. K. Collinge, and D. M. Wagner. 2021. No evidence for enzootic plague within black-tailed prairie dog (*Cynomys ludovicianus*) populations. Integrative Zoology 16:834-851. https://doi.org/10.1111/1749-4877.12546

Coues, E. 1877. Fur-bearing animals: a monograph of North American Mustelidae. Department of Interior USGS Miscellaneous Publication.

Cully, J. F., Jr., S. K. Collinge, R. E. VanNimwegen, C. Ray, W. C. Johnson, B. Thiagarajan, D. B. Conlin, and B. E. Holmes. 2010. Spatial variation in keystone effects: small mammal diversity associated with black-tailed prairie dog colonies. Ecography 33:667-677. https://doi.org/10.1111/j.1600-0587.2009.05746.x

Cully, J. F., Jr., and E. S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82:894-905. https://doi.org/10.1644/1545-1542(2001)082<0894:ICOSPI>2.0.CO;2

Dierenfeld, E. S., K. Whitehouse-Tedd, V. Dermauw, L. R. Hanebury, and D. E. Biggins. 2021. Environmental and prey-based factors underpinning variability in prairie dogs eaten by black-footed ferrets. Ecosphere 12(1):e03316. https://doi.org/10.1002/ecs2.3316

Dombro, L. M. 2016. Ecological effects of deltamethrin insecticide in prairie dog colonies of western South Dakota. M.S. Thesis, Auburn University, Alabama. http://etd.auburn.edu/handle/10415/5005

Eads, D., T. Livieri, T. Tretten, J. Hughes, N. Kaczor, E. Halsell, S. Grassel, P. Dobesh, E. Childers, D. Lucas, L. Noble, M. Vasquez, A. C. Grady, and D. Biggins. 2022. Assembling a safe and effective toolbox for integrated flea control and plague mitigation: fipronil experiments with prairie dogs. PLoS ONE 17(8): e0272419. https://doi.org/10.1371/journal.pone.0272419

Eads, D. A. 2012. Notes on behaviors of free-ranging black-footed ferrets: Conata Basin South Dakota 2007–2009. Western North American Naturalist 72:191–195. https://doi.org/10.3398/064.072.0208

Eads, D. A., and D. E. Biggins. 2015. Plague bacterium as a transformer species in prairie dogs and the grasslands of western North America. Conservation Biology 29:1086-1093. https://doi.org/10.1111/cobi.12498

Eads, D. A., D. E. Biggins, J. Bowser, K. Broerman, T. M. Livieri, E. Childers, P. Dobesh, and R. L. Griebel. 2019. Evaluation of five pulicides to suppress fleas on black-tailed prairie dogs: encouraging long-term results with systemic 0.005% fipronil. Vector-Borne and Zoonotic Diseases 19:400-406. https://doi.org/10.1089/vbz.2018.2339

Eads, D. A., D. E. Biggins, J. Bowser, J. C. McAllister, R. L. Griebel, E. Childers, T. M. Livieri, C. Painter, L. Sterling Krank, and K. Bly. 2018. Resistance to deltamethrin in prairie dog (*Cynomys ludovicianus*) fleas in the field and in the laboratory. Journal of Wildlife Diseases 54:745-754. https://doi.org/10.7589/2017-10-250

Eads, D. A., D. E. Biggins, and K. L. Gage. 2020. Ecology and management of plague in diverse communities of rodents and fleas. Vector-Borne and Zoonotic Diseases 20:888-896. https://doi.org/10.1089/vbz.2020.2625

Eads, D. A., D. E. Biggins, and T. M. Livieri. 2015. Spatial and temporal use of a prairie dog colony by coyotes and rabbits: potential indirect effects on endangered black-footed ferrets. Journal of Zoology 296:146-152. https://doi.org/10.1111/jzo.12228

Eads, D. A., J. Bowser, M. Poonamallee, S. Molina, J. Neill, and L. White. 2016. Black-tailed prairie dogs selectively urinate near rabbit urine: the scent of competition between a rodent and a lagomorph? Ethology Ecology & Evolution 28:102-109. https://doi.org/10.1080/03949370.2014.999828

Eads, D. A., T. M. Livieri, P. Dobesh, E. Childers, L. E. Noble, M. C. Vasquez, and D. E.

Biggins. 2021. Fipronil pellets reduce flea abundance on black-tailed prairie dogs: potential tool for plague management and black-footed ferret conservation. Journal of Wildlife Diseases 57:434-438. https://doi.org/10.7589/JWD-D-20-00161

Eisen, R. J., J. L. Holmes, A. M. Schotthoefer, S. M. Vetter, J. A. Montenieri, and K. L. Gage. 2008. Demonstration of early-phase transmission of *Yersinia pestis* by the mouse flea, *Aetheca wagneri* (Siphonaptera: Ceratophylidae), and implications for the role of deer mice as enzootic reservoirs. Journal of Medical Entomology 45:1160-1164. https://doi.org/10.1093/jmedent/45.6.1160

Fox, N. S., S. C. Wallace, and J. I. Mead. 2017. Fossil *Mustela nigripes* from Snake Creek Burial Cave, Nevada, and implications for black-footed ferret paleoecology. Western North American Naturalist 77:137-151. https://doi.org/10.3398/064.077.0202

Gage, K. L., and M. Y. Kosoy. 2005. Natural history of plague: Perspectives from more than a century of research. Annual Review of Entomology 50:505-528. https://doi.org/10.1146/annurev.ento.50.071803.130337

Godbey, J. L., D. E. Biggins, and D. Garelle. 2006. Exposure of captive black-footed ferrets to plague and implications for species recovery. Pages 233-237 in J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret – progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293. https://doi.org/10.3133/sir20055293

Goldberg, A. R., D. E. Biggins, S. Ramakrishnan, J. W. Bowser, C. J. Conway, D. A. Eads, and J. Wimsatt. 2022a. Deltamethrin reduces survival of non-target small mammals. Wildlife Research 49:698-708. https://doi.org/10.1071/WR21153

Goldberg, A. R., D. A. Eads, and D. E. Biggins. 2022b. Plague circulation in small mammals elevates extinction risk for the endangered Peñasco least chipmunk. Global Ecology and Conservation 38:e02244. https://doi.org/10.1016/j.gecco.2022.e02244

Harris, N. C., T. M. Livieri, and R. R. Dunn. 2014. Ectoparasites in black-footed ferrets (*Mustela nigripes*) from the largest reintroduced population of the Conata Basin, South Dakota, USA. Journal of Wildlife Diseases 50:340-343. https://doi.org/10.7589/2013-03-048

Henderson, F. R., P. F. Springer, and R. Adrian. 1969. The black-footed ferret in South Dakota. South Dakota Game, Fish and Parks Technical Bulletin No. 4. Pierre, South Dakota.

Hoogland, J. L. 1996. *Cynomys ludovicianus*. Mammalian Species 535:1-10. https://doi.org/10.2307/3504202

Livieri, T. M. 2007. Black-footed ferret spatial use of prairie dog colonies in South Dakota. M.S. Thesis, University of Wisconsin-Stevens Point, Wisconsin. http://digital.library.wisc.edu/1793/81176

Maestas, L. P., and H. B. Britten. 2019. Effects of deltametrhin treatment on small mammal and ectoparasite population dynamics and plague prevalence in a North American mixed-grass prairie system. Vector-Borne and Zoonotic Diseases 19:274-283. https://doi.org/10.1089/vbz.2018.2332

Matchett, M. R., D. E. Biggins, V. Carlson, B. Powell and T. Rocke. 2010. Enzootic plague reduces black-footed ferret (*Mustela nigripes*) survival in Montana. Vector-Borne and Zoonotic Diseases 10:27-35. https://doi.org/10.1089/vbz.2009.0053

Matchett, M. R., D. A. Eads, J. Cordova, T. M. Livieri, H. Hicks, and D. E. Biggins. 2023. Flea control on prairie dogs (*Cynomys* spp.) with fipronil bait pellets: potential plague mitigation tool for rapid field application and wildlife conservation. Journal of Wildlife Diseases 59:71-83. https://doi.org/10.7589/JWD-D-22-00008

Matchett, M. R., T. R. Stanley, M. F. Mccollister, D. A. Eads, J. T. Boulerice, and D. E. Biggins. 2021. Oral sylvatic plague vaccine does not adequately protect prairie dogs (*Cynomys* spp.) for endangered black-footed ferret (*Mustela nigripes*) conservation. Vector-Borne and Zoonotic Diseases 21:921-940.

Millar, J. S. 1985. Life cycle characteristics of *Peromyscus maniculatus nebrascensis*. Canadian Journal of Zoology 63:1280-1284. https://doi.org/10.1139/z85-191

Monk, J. D., J. A. Smith, E. Donadio, P. L. Perrig, R. D. Crego, M. Fileni, O. Bidder, S. A. Lambertucci, J. N. Pauli, O. J. Schmitz, and A. D. Middleton. 2022. Cascading effects of a disease outbreak in a remote protected area. Ecology Letters 25:1152-1163. https://doi.org/10.1111/ele.13983

Monterroso, P., G. Garrote, A. Serronha, E. Santos, M. Delibes-Mateos, J. Abrantes, R. Perez de Ayala, F. Silvestre, J. Carvalho, I. Vasco, A. M. Lopes, E. Maio, M. J. Magalhaes, L. S. Mills, P. J. Esteves, M. A. Simon, and P. C. Alves. 2016. Disease-mediated bottom-up regulation: an emergent virus affects a keystone prey, and alters the dynamics of trophic webs. Scientific Reports 6:1-9. https://doi.org/10.1038/srep36072

Owen, P. R., C. J. Bell, and E. M. Mead. 2000. Fossils, diet, and conservation of black-footed ferrets (*Mustela nigripes*). Journal of Mammalogy 81:422-433. https://doi.org/10.1644/1545-1542(2000)081<0422:FDACOB>2.0.CO;2

Pauli, J. N., S. W. Buskirk, E. S. Williams, and W. H. Edwards. 2006. A plague epizootic in the black-tailed prairie dog (*Cynomys ludovicianus*). Journal of Wildlife Diseases 42:74-80. https://doi.org/10.7589/0090-3558-42.1.74

Phillips, D. L., R. Inger, S. Bearhop, A. L. Jackson, J. W. Moore, A. C. Parnell, B. X. Semmens, and E. J. Ward. 2014. Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology 92:823–835. https://doi.org/10.1139/cjz-2014-0127

Phillips, P., T. M. Livieri, and B. J. Swanson. 2020. Genetic signature of disease epizootic and reintroduction history in an endangered carnivore. Journal of Mammalogy 101:779-789. https://doi.org/10.1093/jmammal/gyaa043

Rocke, T. E., J. Mencher, S. R. Smith, A. M. Friedlander, G. P. Andrews, and L. A. Baeten. 2004. Recombinant F1-V fusion protein protects black-footed ferrets (*Mustela nigripes*) against virulent *Yersinia pestis* infection. Journal of Zoo and Wildlife Medicine 35:142-146. https://doi.org/10.1638/03-021

Rocke, T. E., S. Smith, P. Marinari, J. Kreeger, J. T. Enama, and B. S. Powell. 2008. Vaccination with F1-V fusion protein protects black-footed ferrets (*Mustela nigripes*) against plague upon oral challenge with *Yersinia pestis*. Journal of Wildlife Diseases 44:1-7. https://doi.org/10.7589/0090-3558-44.1.1

Russell, R. E., R. C. Abbott, D. W. Tripp, and T. E. Rocke. 2018. Local factors associated with on-host flea distributions on prairie dog colonies. Ecology and Evolution 8:8951-8972. https://doi.org/10.1002/ece3.4390

Salkeld, D. J., and P. Stapp. 2008. Prevalence and abundance of fleas in black-tailed prairie dog burrows: implications for the transmission of plague (*Yersinia pestis*). Journal of Parasitology 94:616-621. https://doi.org/10.1645/GE-1368.1

Santymire, R. M., S. M. Wisely, T. M. Livieri, and J. Howard. 2012. Using canine width to determine age in the black-footed ferret *Mustela nigripes*. Small Carnivore Conservation 46:17-21. https://smallcarnivoreconservation.com/index.php/sccg/issue/view/276/78

Sheets, R. G., R. L. Linder, and R. B. Dahlgren. 1972. Food habits of two litters of black-footed ferrets in South Dakota. American Midland Naturalist 87:249-251. https://doi.org/10.2307/2423900

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663-688. https://doi.org/10.1093/jmammal/gyw078

Smith, K. F., K. Acevedo-Whitehouse, and A. B. Pedersen. 2009. The role of infectious diseases in biological conservation. Animal Conservation 12:1-12. https://doi.org/10.1111/j.1469-1795.2008.00228.x

Stephens, R. B., A. P. Ouimette, E. A. Hobbie, and R. J. Rowe. 2022. Reevaluating trophic discrimination factors (Δδ13C and Δδ15N) for diet reconstruction. Ecological Monographs 92(3):e1525. https://doi.org/10.1002/ecm.1525

Stock, B. C., A. L. Jackson, E. J. Ward, A. C. Parnell, D. L. Phillips, and B. X. Semmens. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 2018:e5096. https://doi.org/10.7717/peerj.5096

Thiagarajan, B., J. F. Cully Jr., T. M. Loughin, J. A. Montenieri, and K. L. Gage. 2008. Geographic variation in rodent-flea relationships in the presence of black-tailed prairie dog colonies. Journal of Vector Ecology 33:178-190. https://doi.org/10.3376/1081-1710(2008)33[178:GVIRRI]2.0.CO;2

Tompkins, D. M., A. M. Dunn, M. J. Smith, and S. Telfer. 2011. Wildlife diseases: from individuals to ecosystems. Journal of Animal Ecology 80:19-38. https://doi.org/10.1111/j.1365-2656.2010.01742.x

Tretten, T. N. 2019. Rarely observed behaviors and occurrences of black-footed ferrets preconditioning for wild release 2014-2017. Journal of Fish and Wildlife Management 10:241-249. https://doi.org/10.3996/042018-JFWM-030

Tripp, D. W., T. E. Rocke, J. P. Runge, R. C. Abbott, and M. W. Miller. 2017. Burrow dusting or oral vaccination prevents plague-associated prairie dog colony collapse. EcoHealth 14:451-462. https://doi.org/10.1007/s10393-017-1236-y

U. S. Fish and Wildlife Service. 2019. Species status assessment report for the black-footed ferret (*Mustela nigripes*). Carr, Colorado. https://ecos.fws.gov/ServCat/DownloadFile/169265

Windell, R. M., L. L. Bailey, T. M. Livieri, D. A. Eads, D. E. Biggins, and S. W. Breck. In review. Coyote use of prairie dog colonies is most frequent in areas used by American badgers. Journal of Mammalogy 000:000-000.

Wobeser, G., M. Ngeleka, G. Appleyard, L. Bryden, and M. R. Mulvey. 2007. Tularemia in deer mice (*Peromyscus maniculatus*) during a population irruption in Saskatchewan, Canada. Journal of Wildlife Diseases 43:23-31. https://doi.org/10.7589/0090-3558-43.1.23

APPENDIX

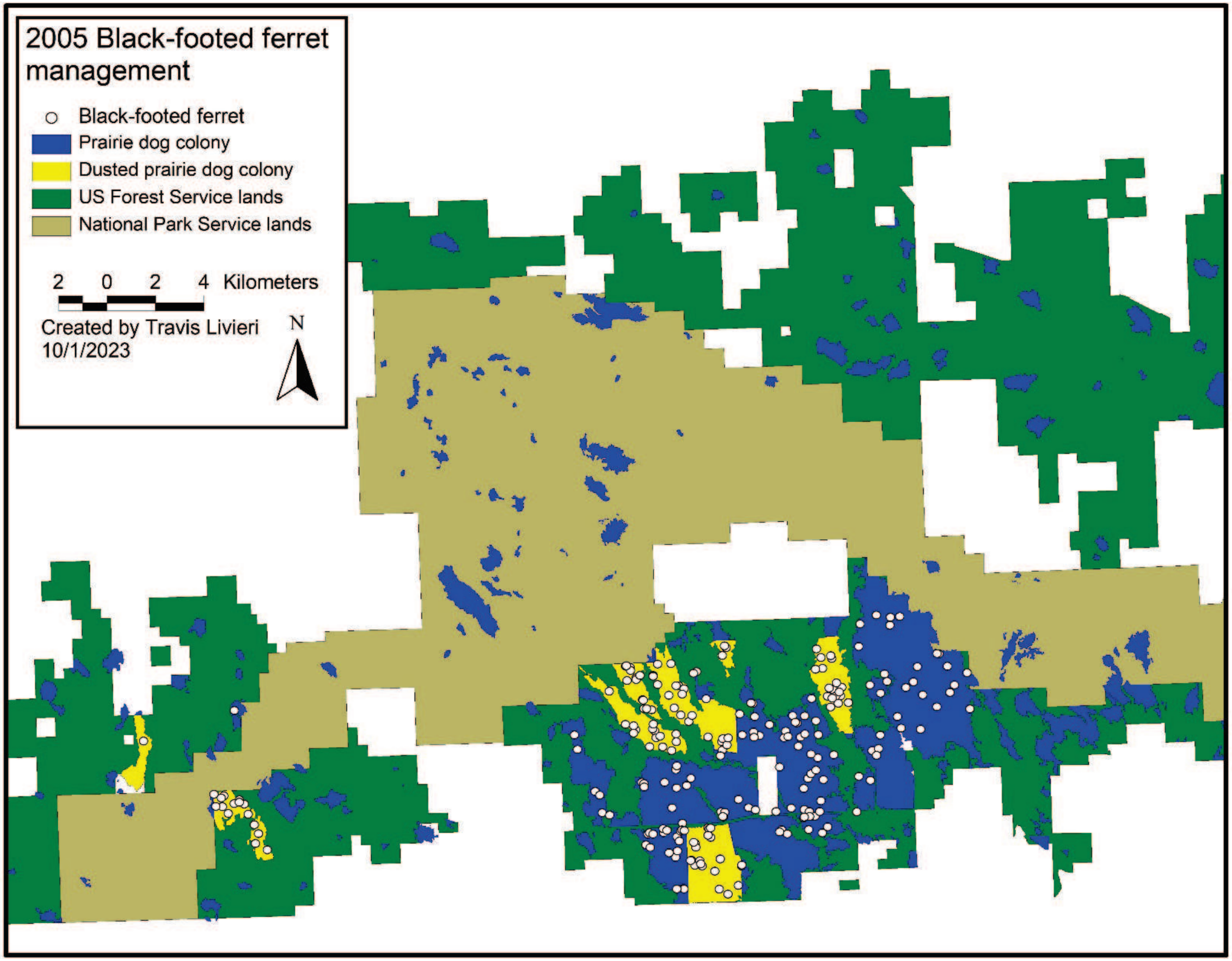

Figure S1: Black-tailed prairie dog colonies, black-footed ferrets and insecticide dust treatment in 2005 at Conata Basin/Badlands National Park, South Dakota.

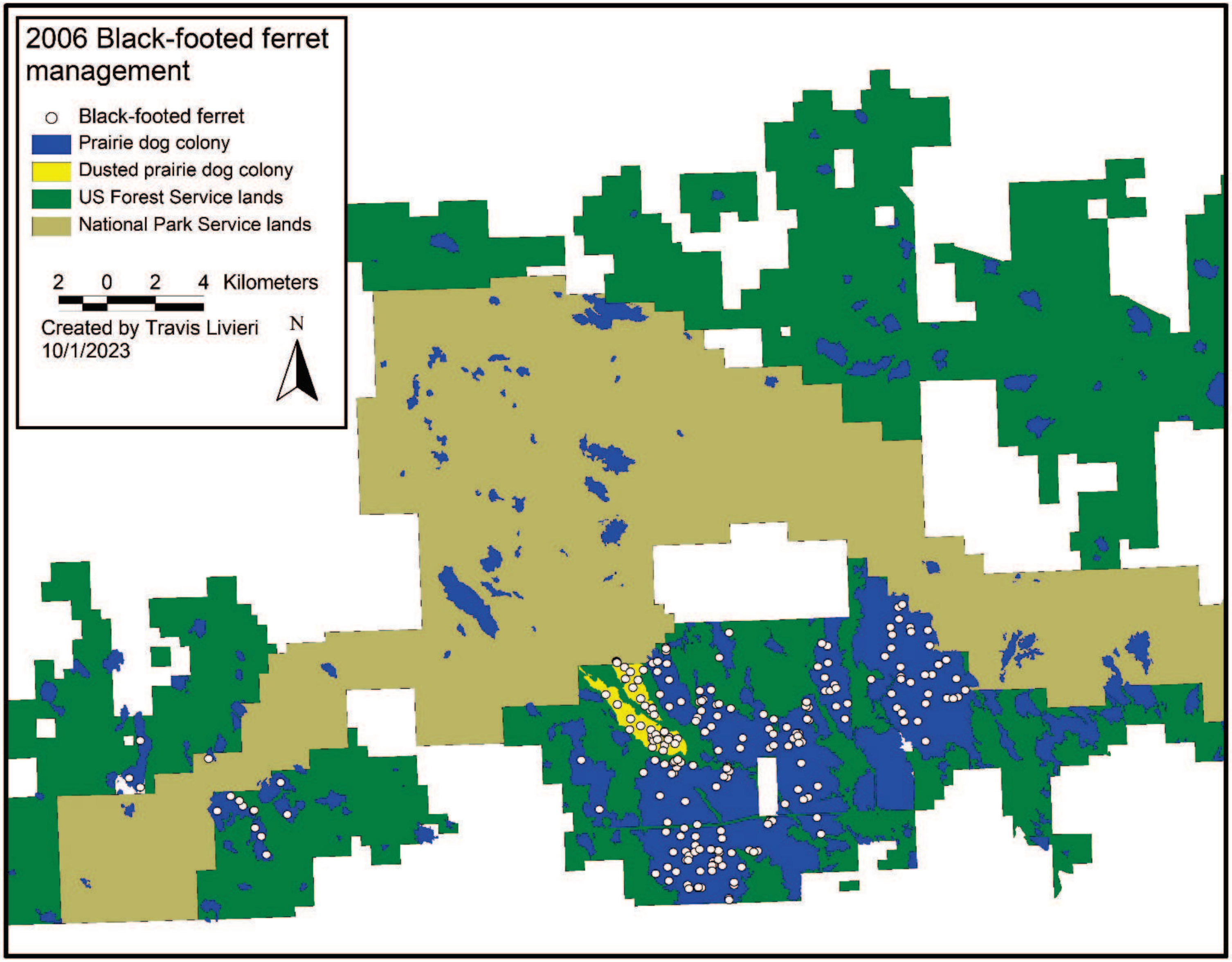

Figure S2: Black-tailed prairie dog colonies, black-footed ferrets and insecticide dust treatment in 2006 at Conata Basin/Badlands National Park, South Dakota.

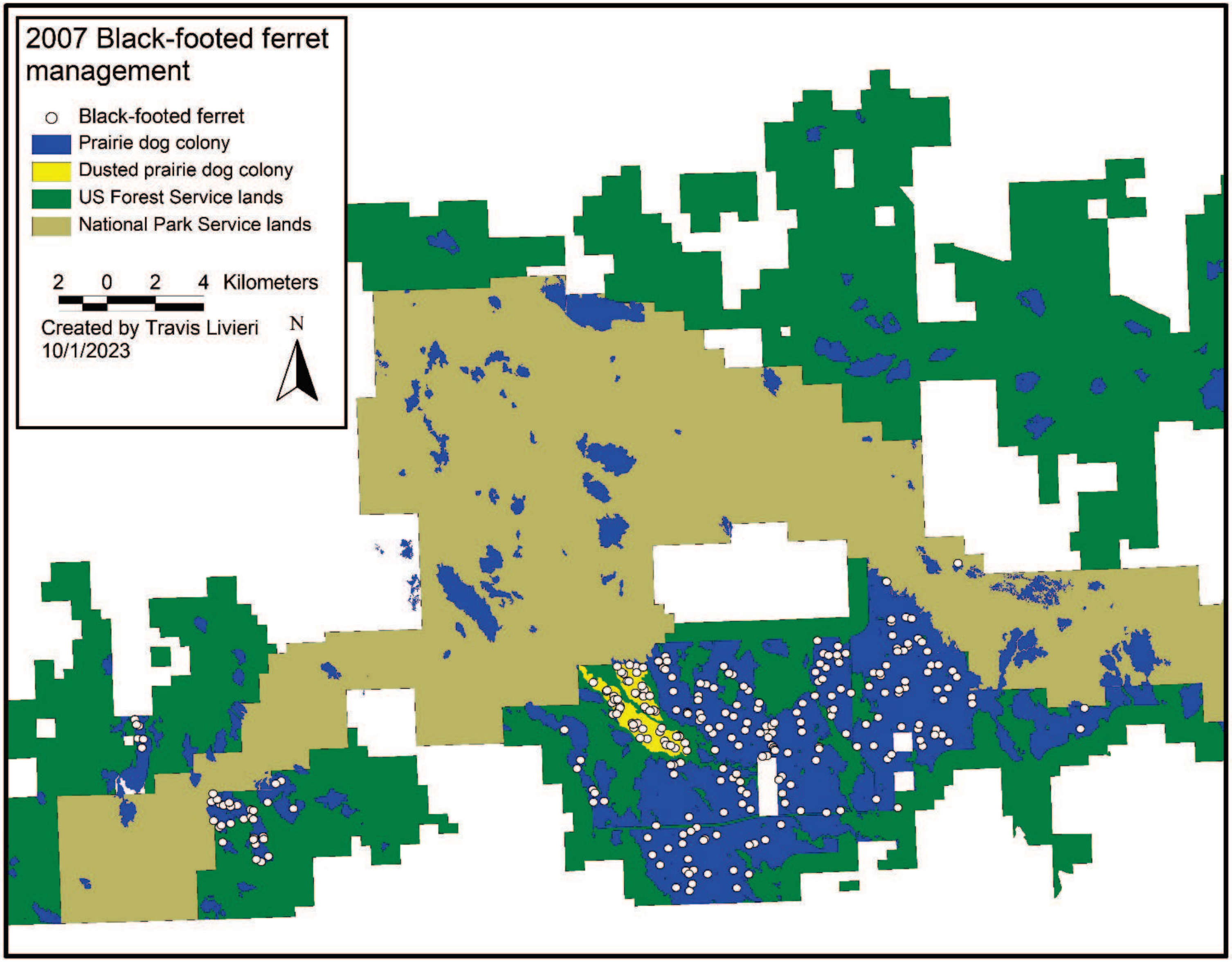

Figure S3: Black-tailed prairie dog colonies, black-footed ferrets and insecticide dust treatment in 2007 at Conata Basin/Badlands National Park, South Dakota.

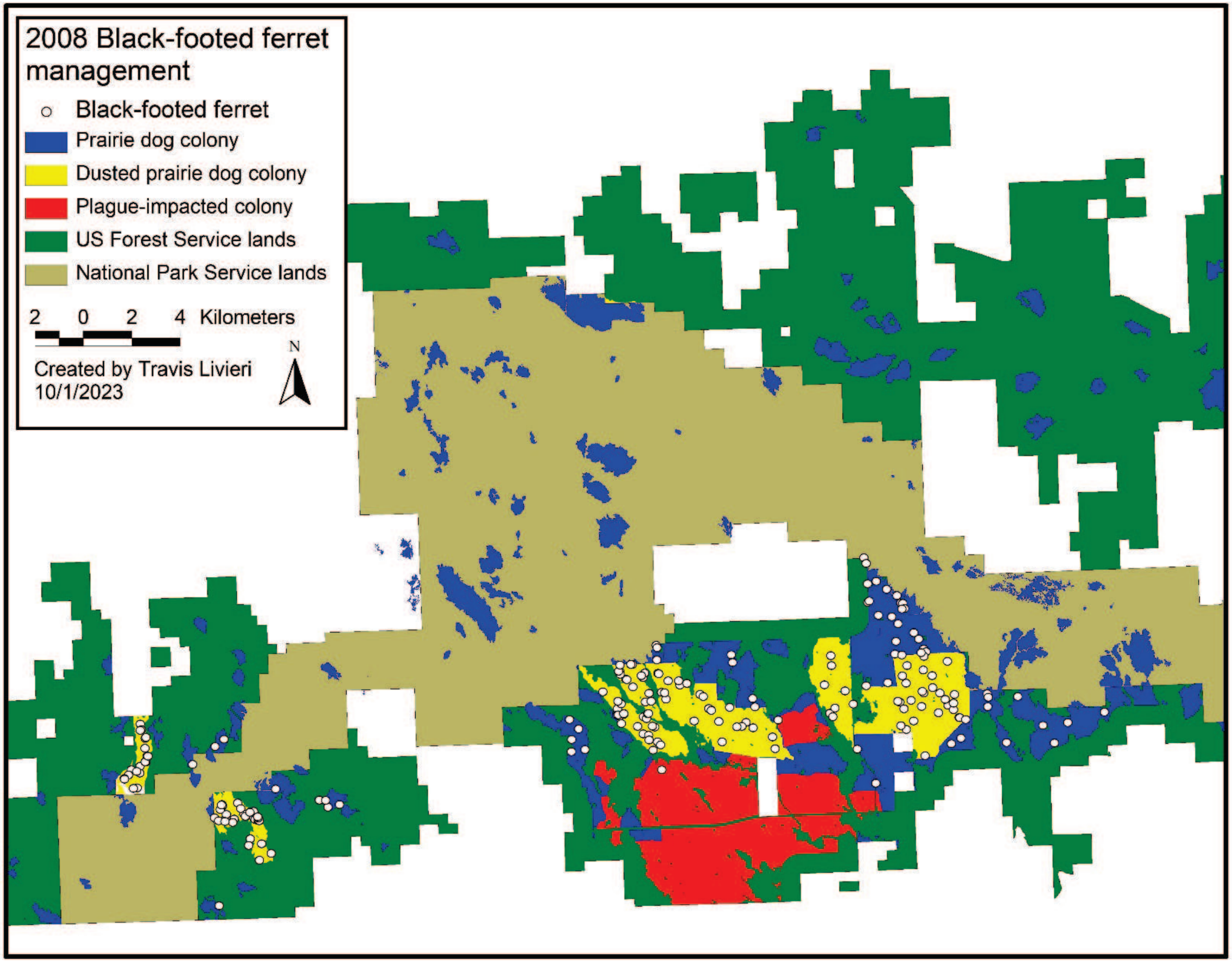

Figure S4: Black-tailed prairie dog colonies, black-footed ferrets, insecticide dust treatment, and plague-impacted colonies in 2008 at Conata Basin/Badlands National Park, South Dakota.

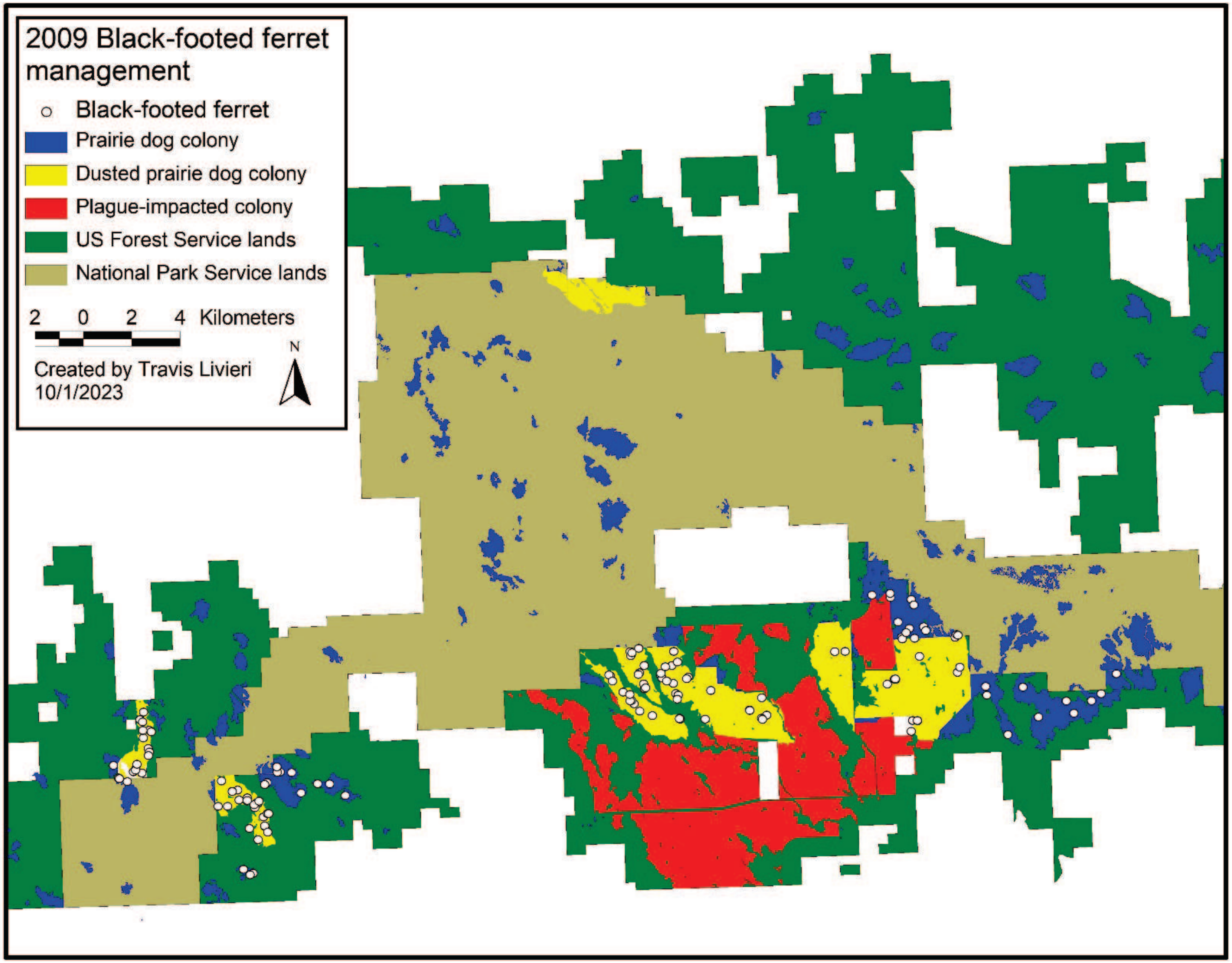

Figure S5: Black-tailed prairie dog colonies, black-footed ferrets, insecticide dust treatment, and plague-impacted colonies in 2009 at Conata Basin/Badlands National Park, South Dakota.

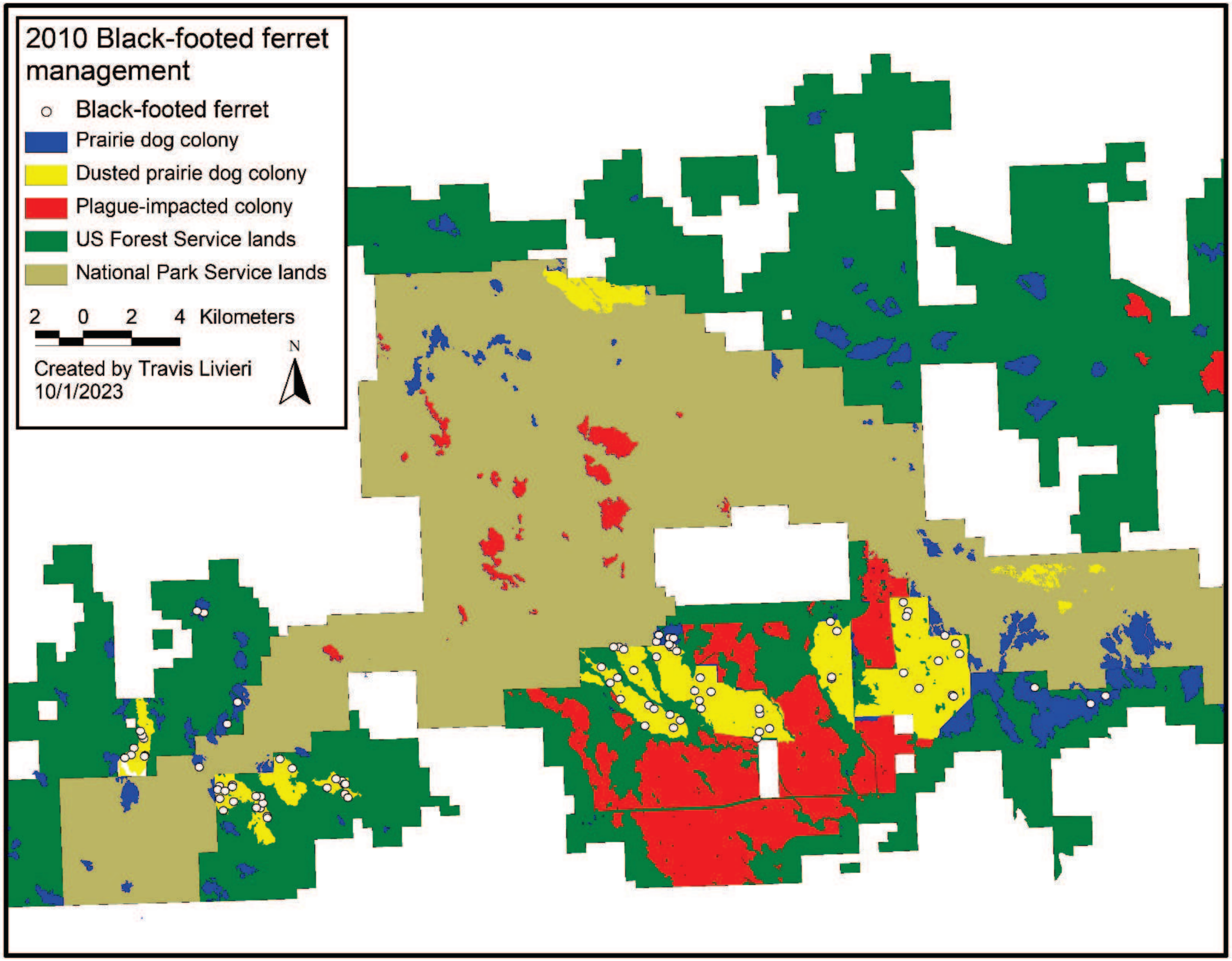

Figure S6: Black-tailed prairie dog colonies, black-footed ferrets, insecticide dust treatment, and plague-impacted colonies in 2010 at Conata Basin/Badlands National Park, South Dakota.

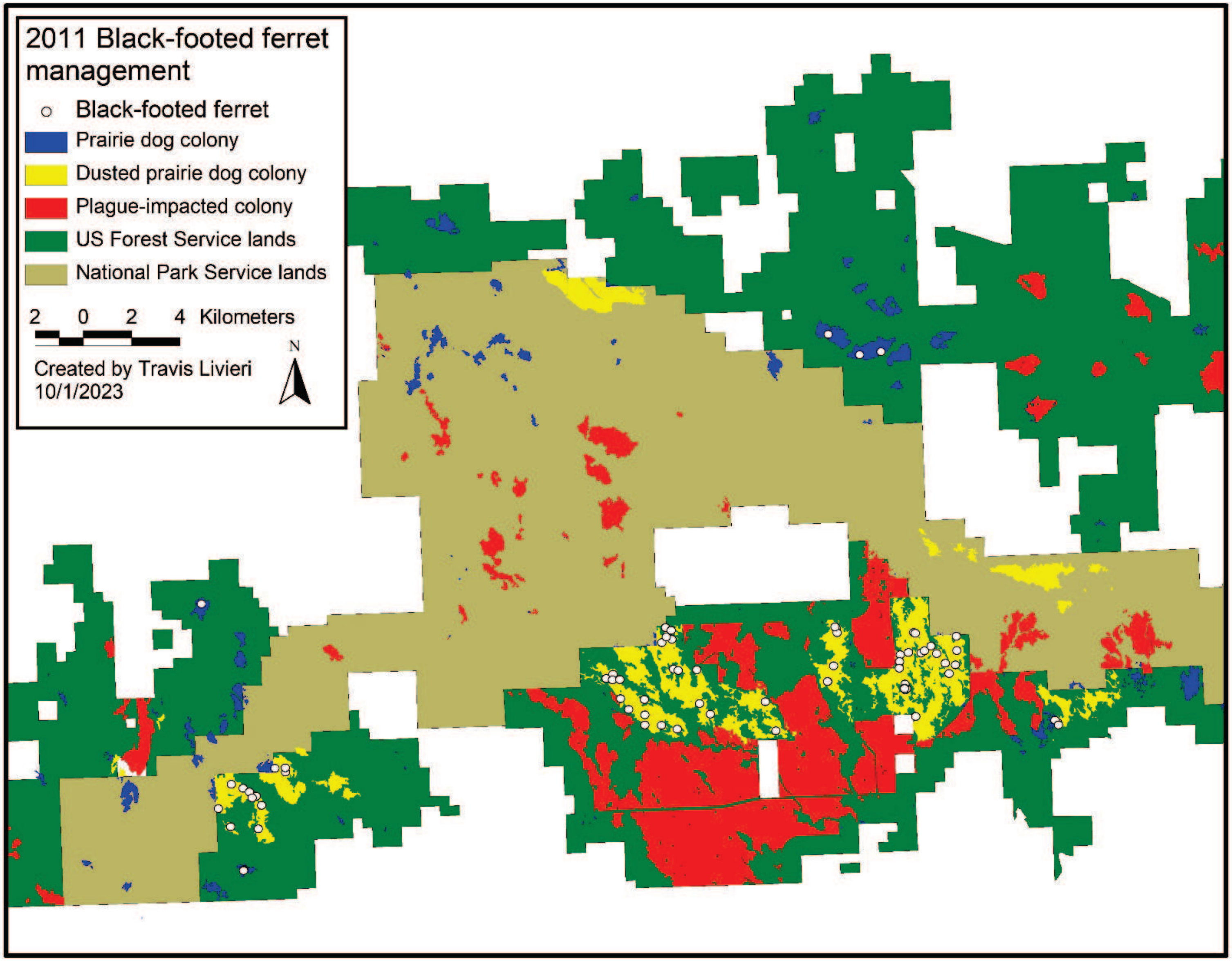

Figure S7: Black-tailed prairie dog colonies, black-footed ferrets, insecticide dust treatment, and plague-impacted colonies in 2011 at Conata Basin/Badlands National Park, South Dakota.

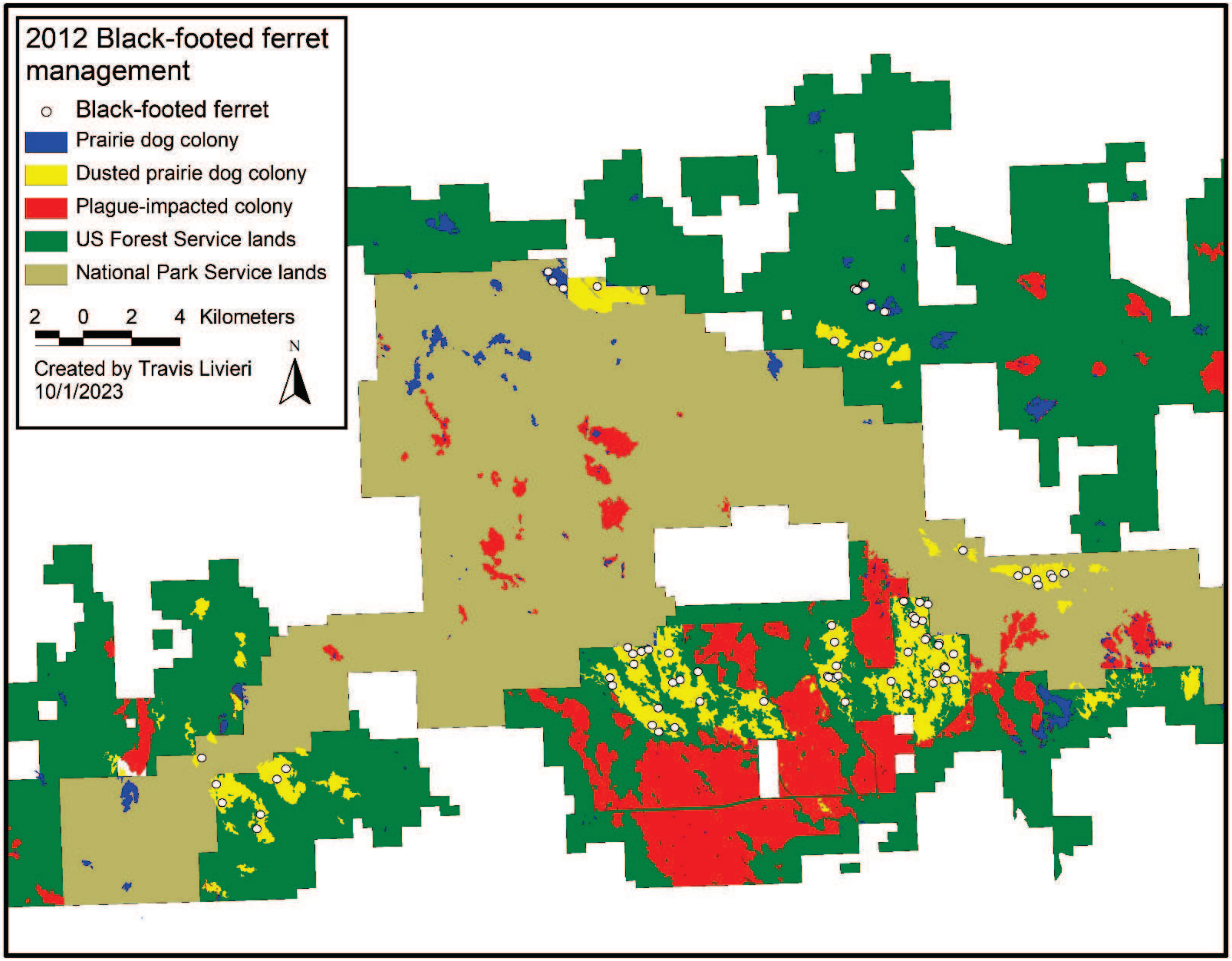

Figure S8: Black-tailed prairie dog colonies, black-footed ferrets, insecticide dust treatment, and plague-impacted colonies in 2012 at Conata Basin/Badlands National Park, South Dakota.

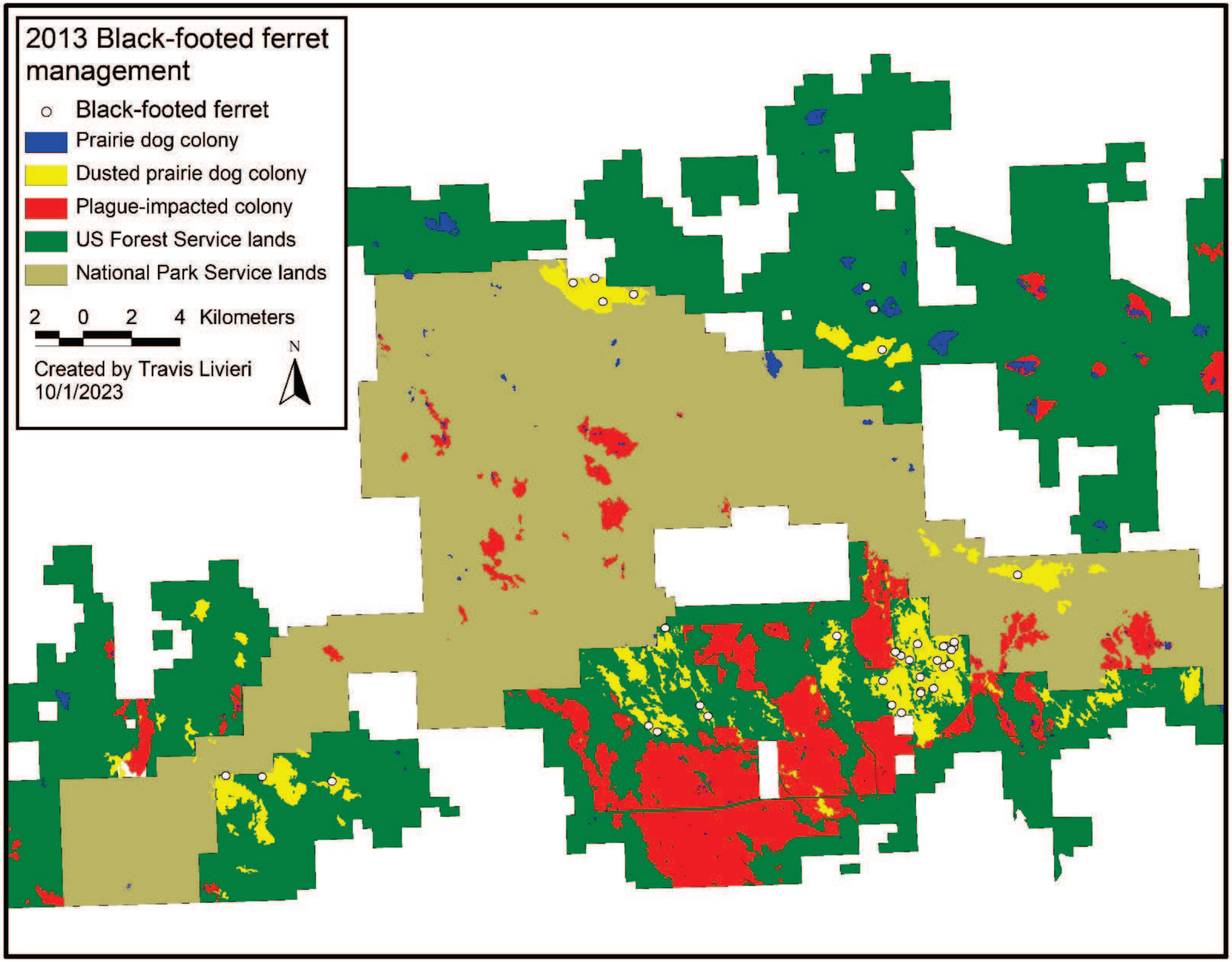

Figure S9: Black-tailed prairie dog colonies, black-footed ferrets, insecticide dust treatment, and plague-impacted colonies in 2013 at Conata Basin/Badlands National Park, South Dakota.

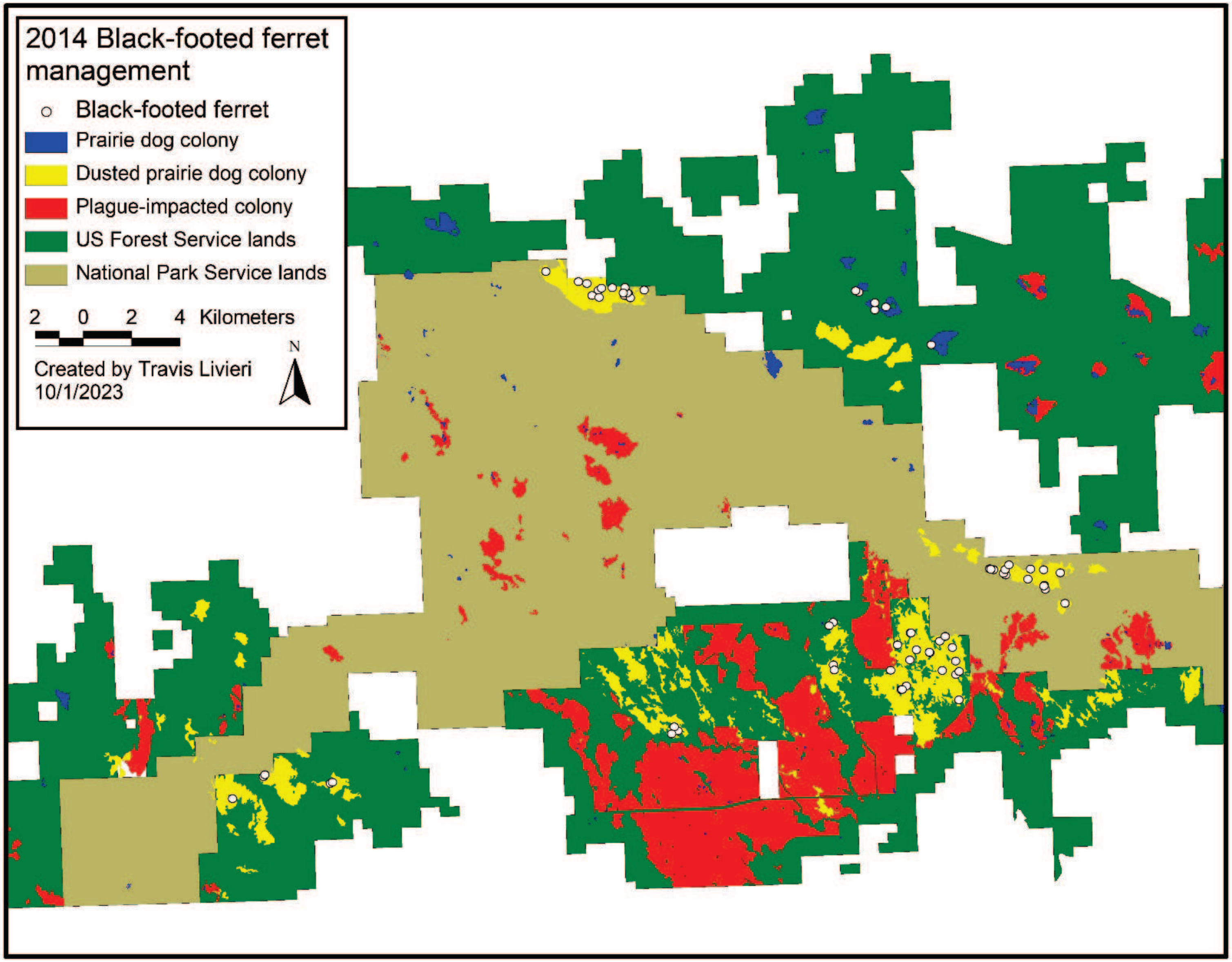

Figure S10: Black-tailed prairie dog colonies, black-footed ferrets, insecticide dust treatment, and plague-impacted colonies in 2014 at Conata Basin/Badlands National Park, South Dakota.

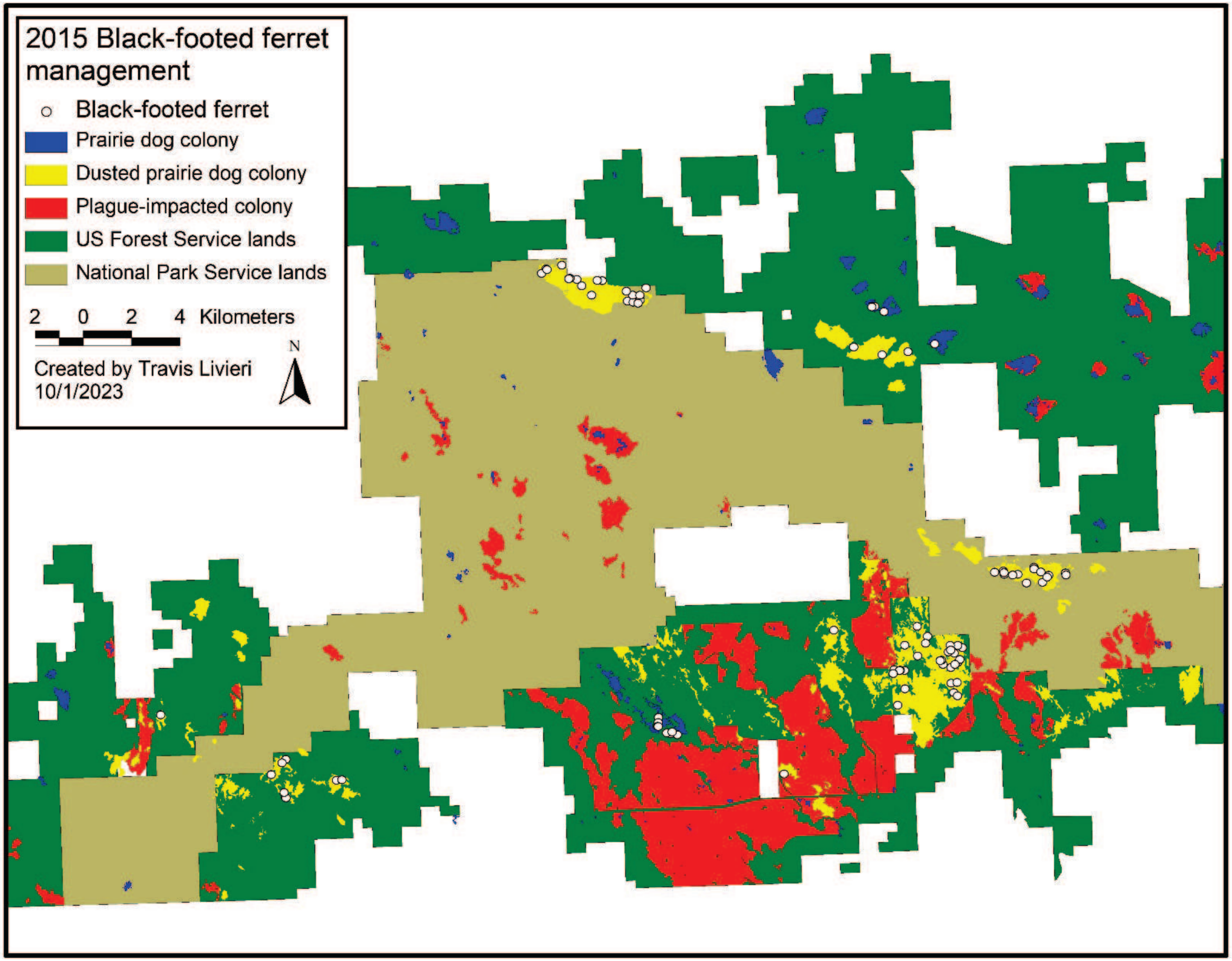

Figure S11: Black-tailed prairie dog colonies, black-footed ferrets, insecticide dust treatment, and plague-impacted colonies in 2015 at Conata Basin/Badlands National Park, South Dakota.

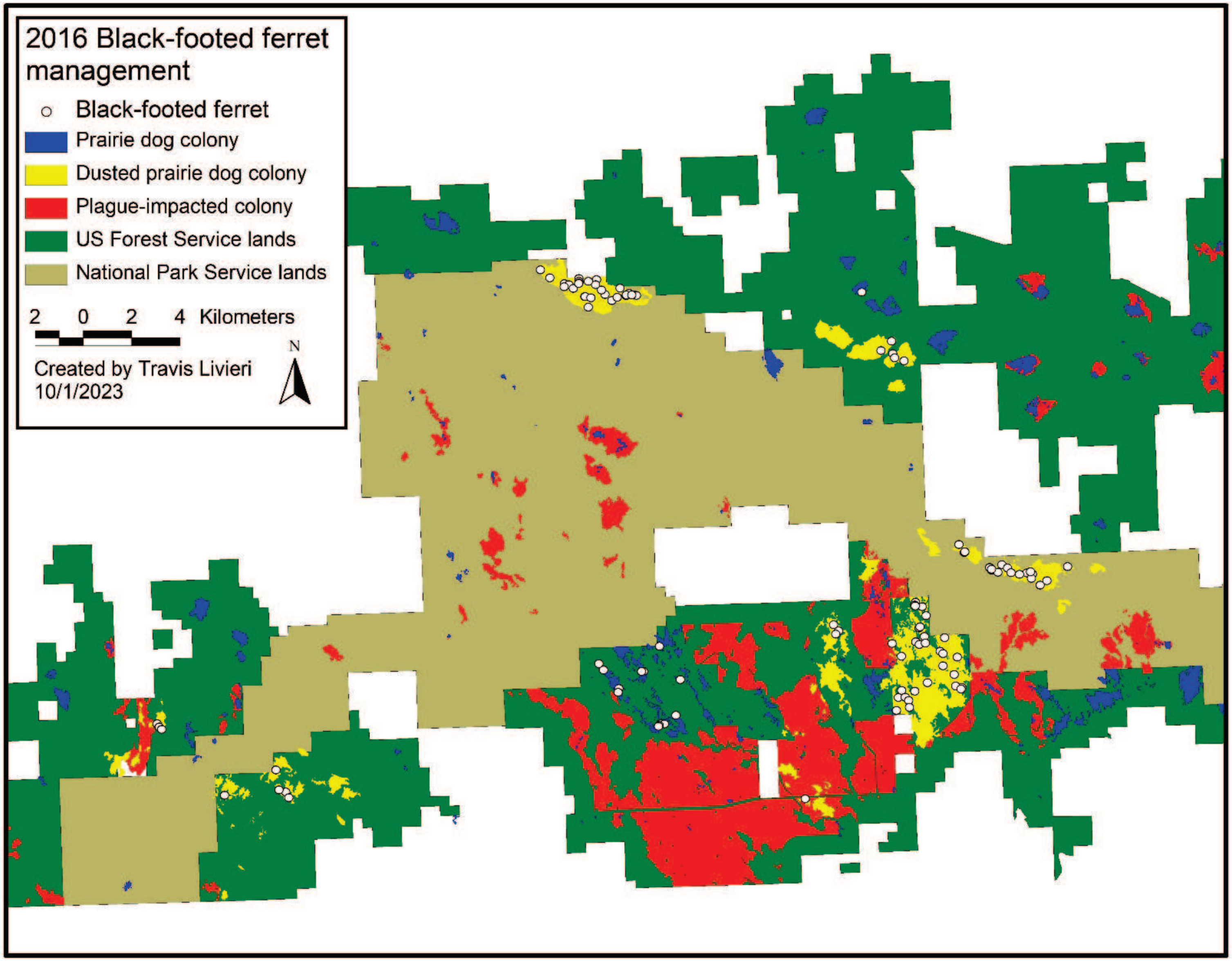

Figure S12: Black-tailed prairie dog colonies, black-footed ferrets, insecticide dust treatment, and plague-impacted colonies in 2016 at Conata Basin/Badlands National Park, South Dakota.

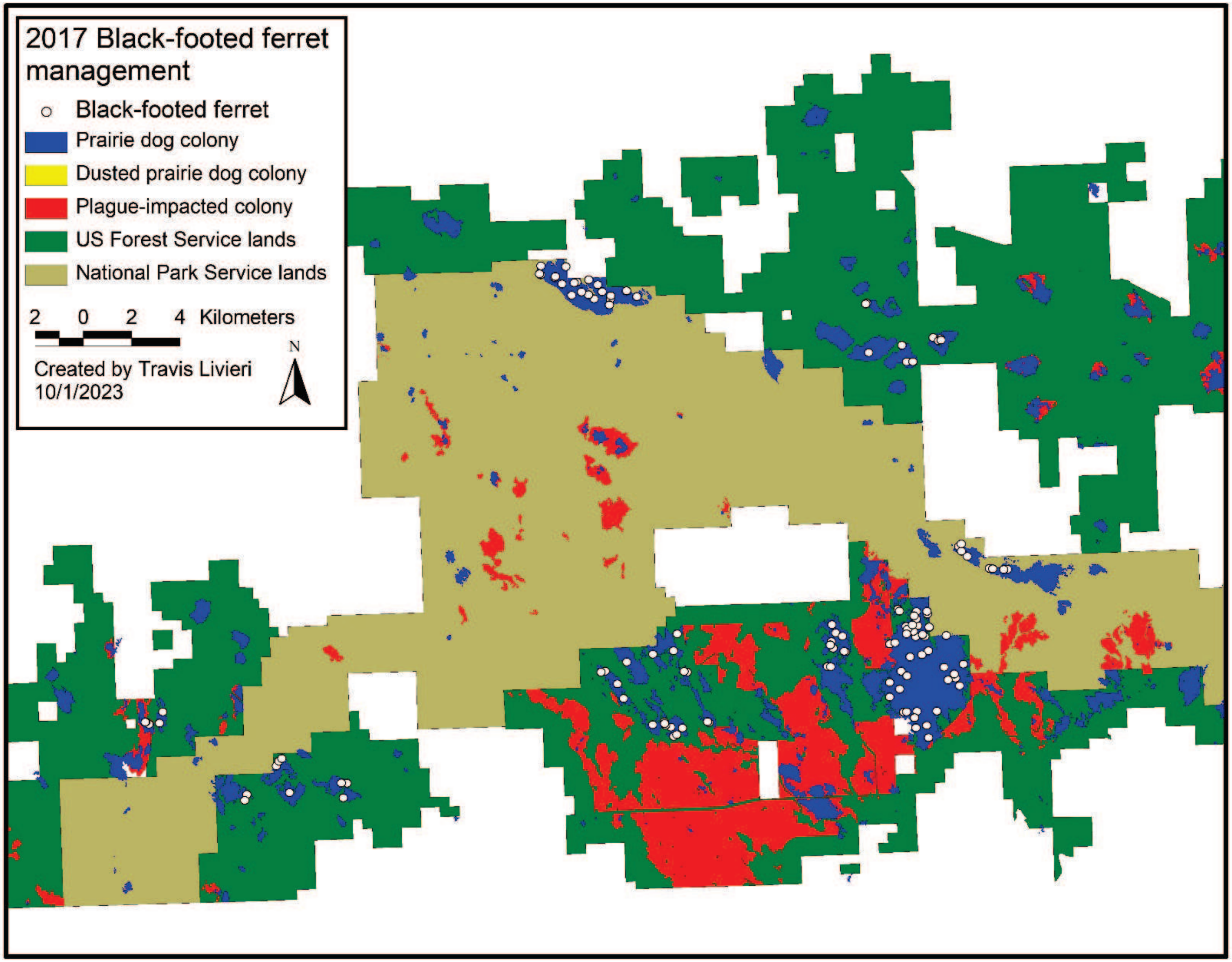

Figure S13: Black-tailed prairie dog colonies, black-footed ferrets, and plague-impacted colonies in 2017 at Conata Basin/Badlands National Park, South Dakota. Insecticide dust treatment continued in 2017 but was not included in this study.