Conserving Endangered Black-Footed Ferrets: Biological Threats, Political Challenges, and Lessons Learned

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Abstract

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 (**Fig. 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. 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 (**Fig. 2**): black-tailed (*C. ludovicianus*; **Fig. 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

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Fig. 1 A black-footed ferret on a prairie dog burrow mound in South Dakota. Photo by Travis Livieri.

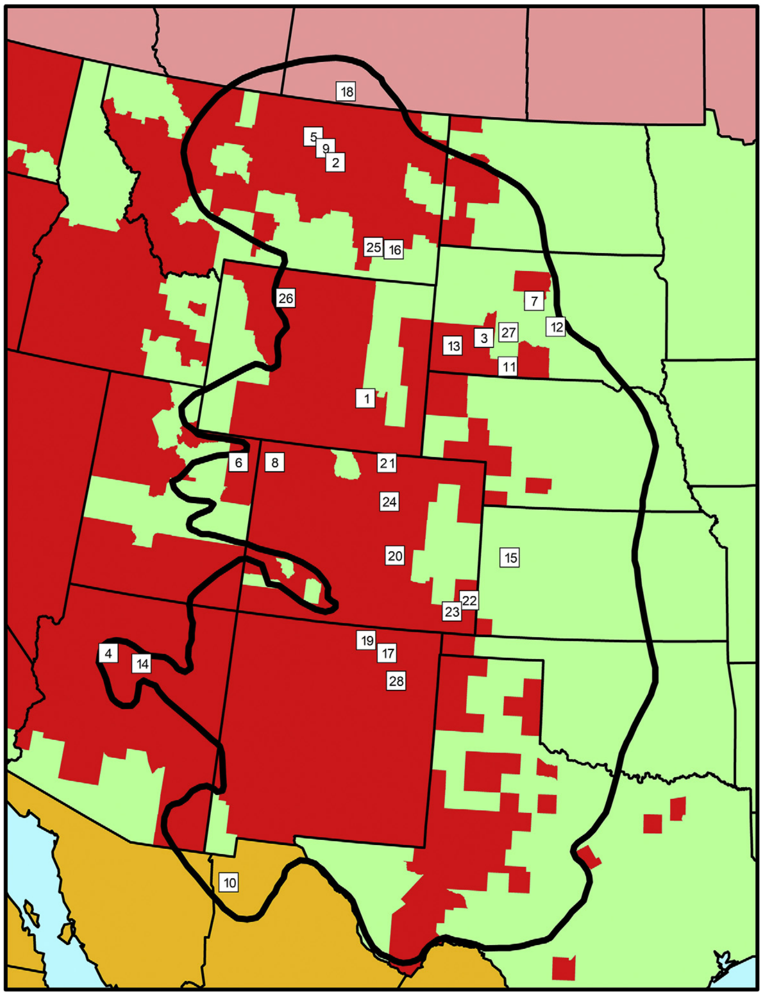

Fig. 2 Historical range of black-footed ferrets (black outline) and reintroduction sites (numbered squares corresponding with Table 1). Counties in red have documented plague in animal or flea samples (partially based on Centers for Disease Control and Prevention data).

Fig. 3 Black-tailed prairie dogs on a burrow mound in Montana. Photo by Travis Livieri.

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). 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 (Fig. 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 (Biggins et al., 2006). In particular, adults concentrate their activities in areas with relatively high densities

Fig. 4 A black-tailed prairie dog colony in Grasslands National Park, Saskatchewan, Canada. Photo by Travis Livieri.

of active prairie dog burrow openings, thus providing them not only with numerous escape routes from predators, but also relatively high prey densities (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 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, although prairie dogs may be more aggressive and thwart black-footed ferret attacks during the day. 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. While this foraging "plasticity" may suggest a broader range of habitat and prey, 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. 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. 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, 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 >2000 km eastward in only 60 years and overtaking a significant portion of the prairie dog and black-footed ferret range (**Fig. 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. 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. 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. 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. 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. 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 and many feared the species was now extinct.

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 2800 ha of white-tailed prairie dog colonies scattered over private and public lands. 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 $\sim$50% to an estimated 58 individuals. 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 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. 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 and Eads, 2017; **Fig. 5**). A revised recovery plan, completed in 1988, guided the breeding program and reintroduction efforts. In 1991, 4 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**). 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). 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 (**Fig. 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. 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,

Fig. 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.

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) have yet to establish self-sustaining black-footed ferret populations that persist without supplementation of additional captive-born animals. 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 (Fig. 2, Table 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.

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 5100 black-footed ferrets have been released at 28 sites in 8 US states, Mexico, and Canada (Table 1). Additionally, translocation of wild-born kits has been used to start new sites or supplement existing sites. 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. Plague also impacts a wide variety of wildlife directly and indirectly, primarily via lethal impacts on rodents and lagomorphs (Eads and Biggins, 2015). In Asian ecosystems where animals evolved with plague, the disease plays a role in the cyclic dynamics

Table 1 Black-footed ferret reintroduction sites, corresponding with Fig. 2, including site characteristics and history.

Site (number corresponds to map Fig. 2)	*State or province*	*Year initiated*	*Ownership*	*Prairie dog species*[a]	*Potential or maximum size of prairie dog area*[b]	*Total # of release years*	*Total # black-footed ferrets released*	*Estimated # black-footed ferrets in fall 2019*[c]	*Highest annual estimated # of black-footed ferrets (year)*[d]
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)

Table 1 Black-footed ferret reintroduction sites, corresponding with Fig. 2, including site characteristics and history.—cont'd

Site (number corresponds to map Fig. 2)	*State or province*	*Year initiated*	*Ownership*	*Prairie dog species*[a]	*Potential or maximum size of prairie dog area*[b]	*Total # of release years*	*Total # black-footed ferrets released*	*Estimated # black-footed ferrets in fall 2019*[c]	*Highest annual estimated # of black-footed ferrets (year)*[d]
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	5411	315	1520

Data based partially on USFWS (2019).
[a]Prairie dog species: BTPD = black-tailed prairie dog, WTPD = white-tailed prairie dog, GPD = Gunnison's prairie dog.
[b]Potential or maximum recorded size of prairie dog colony area: Small ≤2000 ha, Medium = 2000–10,000 ha, Large = 10,000–50,000 ha, X-Large ≥50,000 ha.
[c]Minimum number alive estimate based upon annual spotlighting surveys, includes non-breeding age kits.
[d]Highest minimum number alive observed, includes non-breeding age kits.

of mammal populations. However, in naïve ecosystems like North America, plague can be particularly disruptive. 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. 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. 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

Fig. 6 Black-footed ferret cages at the National Black-Footed Ferret Conservation Center, Carr, Colorado. Photo by Travis Livieri.

the bacteria can be fatal. 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 (Fig. 2, Table 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 4000 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 (USFWS, 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; (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 (USFWS, 2019). Research has shown the survival of reintroduced black-footed ferrets is improved through pre-release conditioning of captive-born black-footed ferrets (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 (Fig. 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 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% (USFWS, 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, 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 (USFWS, 2019).

Securing habitat

Black-footed ferret recovery must focus on maintaining and enhancing current recovery sites (**Table 1**) as well as restoring prairie dogs in areas for future recovery sites. The USFWS (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 (USFWS, 2013). Black-footed ferrets currently occupy 97,197 ha of which 12,206 ha are managed for plague at some level (USFWS, 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 <2000 ha of prairie dog colonies and have a very low probability of ever sustaining ≥ 30 breeding adults (Table 1). 18 of the 28 reintroduction sites currently have <2000 hectares of prairie dog colonies. At the nine largest sites, current active prairie dog colony area was only $\sim 25\%$ of the potential or maximum size and 5 of those sites reported no known ferrets in 2019 (USFWS, 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**).

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, effectively relinquishing private property rights of any landowner with prairie dog colonies (USFWS, 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. 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 (Matchett et al., 2010), but it must be applied annually, can be costly, and fleas can develop resistance with repeated applications and under dosing. Recently, a systemic, orally-ingested insecticide bait containing fipronil was registered for use in prairie dogs and demonstrates effective flea control. Fipronil related products have the potential to be more cost effective than deltamethrin 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 (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 (**Fig. 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. 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.

Fig. 7 Black-footed ferret in a live-trap for vaccination against plague in South Dakota. Photo by Travis Livieri.

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 (**Fig. 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? 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**) 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.

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