

The Genetic Legacy of the Black-footed Ferret: Past, Present, and Future

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Abstract

The black-footed ferret (*Mustela nigripes*) evolved in Beringia sometime in the early to middle Pleistocene. By 35,000 years before present the species was distinct from its sister taxon, *Mustela evermannii*. Genetic analysis revealed that historical populations had restricted gene flow prior to human disturbance, which had consequences for the conservation of genetic diversity in the species. Most genetic diversity in the species was lost when Great Plains populations were extirpated, leaving the last surviving population genetically distinct and depauperate. Further genetic losses occurred when almost half of the animals captured from the last population failed to breed in captivity. Once established in captivity, however, maintenance of remaining genetic diversity was within the goals of genetic management mandated by the recovery plan. Reintroduced populations of black-footed ferrets maintained genetic diversity, but were slightly differentiated from one another due to differences in population founders. Wild-born animals were less inbred than captive-released animals, suggesting that inbreeding avoidance mechanisms may operate in the wild. Although much diversity has been lost, inbreeding depression has not been confirmed. Future management efforts should maintain vigilance to conserve remaining genetic diversity both in captivity and in reintroduced populations.

Key words: Captive breeding, genetic diversity, genetic drift, Pleistocene refugia, population bottleneck, reintroduction

Introduction

Eighteen years have passed since the first genetic study of the black-footed ferret (ferret; *Mustela nigripes*) was completed (Kilpatrick and others, 1986). Although techniques have advanced and our understanding of genetic processes has expanded, the story revealed by this species' genes remains unwaveringly clear: the genetic uniformity measured in this species is unprecedented and rivaled by perhaps only one other

carnivore, the African cheetah (*Acinonyx jubatus*; O'Brien and others, 1983). Unlike the cheetah, however, whose Holocene population bottleneck remains shrouded in mystery, the black-footed ferret's demise was witnessed and documented by museum collectors, commercial trappers, animal control agents, and biologists (Anderson and others, 1986), providing a clear understanding of the demography of the bottleneck. Although the dramatic nature of the bottleneck was unfortunate for conservation of the species, it provides conservation-based science with the opportunity to study the genetic consequences of rapid and dramatic population loss outside of the laboratory setting.

Population bottlenecks occur when population size is rapidly reduced; the severity of a bottleneck depends on the minimum population size attained and the duration of time it remains small (Frankham and others, 2002). Although the immediate consequence of small population size is increased risk of extinction due to demographic stochasticity, long-term consequences result from reduced genetic diversity and increased inbreeding (Frankel and Soulé, 1981). By increasing the expression of deleterious alleles, inbreeding reduces individual fitness, further increasing the likelihood of extinction. Inbreeding depression due to a population bottleneck has been documented in a variety of species, including the Florida panther (*Puma concolor coryi*; Roelke and others, 1993), fritillary butterflies (*Melitaea cinxia*; Saccheri and others, 1998), and koalas (*Phascolarctos cinereus*; Seymour and others, 2001). Reduced genetic diversity also has the insidious and difficult to measure effect of reducing a species' ability to adapt to a changing environment. Examples in the literature are few but include endemic rainforest fruitflies (*Drosophila* spp.; Hoffman and others, 2003).

The black-footed ferret experienced serious population decline beginning in the mid to late 1800's as people migrated west and converted grasslands to agriculture. By 1981 only one population remained, and the species reached its nadir in 1987 when the last of 18 individuals were taken into captivity from Meeteetse, Wyoming (Clark, 1994). This was the first time the U.S. Fish and Wildlife Service had managed an endangered species by removing all living individuals from the wild. Ironically, the Service made that decision twice in 1987, when the last remaining California condors (*Gymnogyps*

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californianus; Seal, 1989; Snyder and Snyder, 2000) were also removed from the wild and placed in a captive breeding program. Unfortunately, animal husbandry practices were not fully established in the initial years of captive breeding, and only seven founding ferrets are represented in the current captive population (Garell and others, 1998). Nonetheless, more than 4,000 individuals have been produced, and today approximately 240 animals exist in captivity and 350 in the wild. With a founder genome equivalent (the number of unique genomes represented in the current population) of 4.1 (Russell and others, 1994), the species currently contains a fraction of the genetic diversity once present.

Several demographic events transpired to reduce the population size of this species. Habitat conversion, poisoning campaigns aimed at prairie dogs (*Cynomys* spp.), and exotic diseases decreased the population by 99% over approximately 100 years. In the last historical population, simultaneous epizootics of canine distemper virus and sylvatic plague (*Yersinia pestis*) caused dramatic population decline in less than a year. In order to understand the consequences of these demographic events, one must first understand the context in which they occurred. How much genetic diversity did the species have prior to anthropogenic disturbance? How much genetic diversity did black-footed ferrets have prior to the bottleneck of the Meeteetse population? How did population structure affect the rate of loss of genetic diversity? Once ferrets were taken into a captive breeding program, how well was the remaining genetic diversity conserved? Finally, as reintroduced populations continue to be established, it is crucial to understand how the process of reintroduction affects genetic diversity and structure. In the following chapter I synthesize what is known about the genetic legacy of this species as it passed through the processes of population bottleneck, captive management, and reintroduction.

Pleistocene Colonization of North America

The black-footed ferret is a relatively recent immigrant to North America via the Bering land bridge (Youngman, 1994). The earliest fossil record of a black-footed ferret in North America is from Cathedral Cave in eastern central Nevada (Youngman, 1994). This specimen dates approximately 800,000 years before present based on paleomagnetic data and biochronology of arvicoline rodents collected at the site (Owen and others, 2000). In support of a middle Pleistocene invasion, molecular clock estimates based on 41 isozymes suggest that the black-footed ferret split from its sister species the Siberian polecat (*Mustela eversmannii*) between 0.5 and 2 million years ago (O'Brien and others, 1989). Thus it appears that the proto- black-footed ferret crossed the land bridge approximately 1 to 2 million years ago. The species gained access to the grasslands and shrublands of North America via an interglacial, ice-free corridor (Anderson, 1989;

Youngman, 1994) and was established at least as far south as Nevada by 800,000 years ago. Once established, the species spread rapidly throughout the Great Plains. By 35,000 years before present the black-footed ferret was morphologically distinguishable from *Mustela eversmannii*. In fact, the two species appear to have existed sympatrically; fossils of both species found in eastern Beringia as recently as 35,000 years ago suggest a period of secondary contact after differentiation (Youngman, 1994).

Molecular data suggest that black-footed ferret populations had restricted gene flow and high population differentiation that was influenced by both natural history and the ebb and flow of Pleistocene glaciers (Wisely and others, 2002). Genetic variation becomes partitioned among subpopulations when isolating mechanisms, such as Pleistocene glaciers and unsuitable habitat, prevent gene flow and increase genetic drift (Frankham and others, 2002). Using microsatellite markers, Wisely and others (2002) reported an average F_{ST} of 0.53. F_{ST} is a pairwise measure of genetic variation that is partitioned among populations. This parameter measures genetic structure and gene flow between subpopulations and ranges in value from 0 (no allelic differentiation or structure) to 1 (maximum allelic divergence). The value found for black-footed ferrets is one of the highest reported for a mammalian carnivore and likely reflects aspects of their unusual ecology. Their diminutive body size, coupled with their semi-fossorial lifestyle, likely limited their dispersal capabilities (when compared to other carnivorans) and therefore induced genetic drift within populations and created genetic differentiation among populations (Wisely and others, 2002). Subpopulation isolation was likely exasperated by habitat barriers that formed during glacial maxima.

Historical Genetic Diversity and Structure

The historical population structure of the black-footed ferret in North America greatly influenced the amount of genetic diversity that was lost. The magnitude of loss of genetic diversity was exasperated by the especially isolated nature of the last population. Located on the periphery of the historical distribution near the town of Meeteetse, Wyoming (Hillman and Clark, 1980), this population was likely a refugium during the last glacial maximum and remained isolated from other populations throughout the Holocene (Wisely and others, 2002). Measures of genetic distance used to estimate genetic differences among black-footed ferrets from three historical populations confirm that the Meeteetse population was the most highly differentiated and therefore isolated of the three populations (Wisely and others, 2002). Thus, when ferret populations from the Great Plains were extirpated, the majority of genetic diversity found in the species was lost (table 1, fig. 1). Indeed, the Meeteetse population was different enough from other ferret populations that the addition of even four individuals from Mellette County, South Dakota (the second to

Table 1. Observed (H_o) and expected (H_e) heterozygosities for 14 microsatellite loci in black-footed ferrets from Wyoming, South Dakota, and Kansas combined (representing the species prior to disturbance; $n = 20$), and from Wyoming only ($n = 12$), and HWE P , the probability associated with an exact test of Hardy-Weinberg equilibrium. HWE was tested only in polymorphic loci from the Wyoming population. From Wisely and others (2002). Reprinted with permission of Oxford University Press, Oxford, U.K.

Microsatellite loci names	Wyoming, South Dakota, Kansas		Wyoming only		HWE P
	H_o	H_e	H_o	H_e	
Mvis002	0.65	0.48	0.50	0.39	0.53
Mvis9700	0.33	0.36	0.33	0.39	1
Mvis072	0.47	0.65	0.67	0.58	0.77
Mer095	0.20	0.27	0.17	0.16	1
Mer049	0.35	0.69	0.50	0.51	1
Mvi57	0.10	0.54	0.17	0.16	1
Mvis022	0.11	0.63	0.08	0.23	0.13
Gg4	0.05	0.14	-	-	-
Mvis075	0.17	0.53	-	-	-
Mvi87	0.00	0.43	-	-	-
G1A	0.10	0.19	-	-	-
Mvi232	0.20	0.19	-	-	-
Mer022	0.11	0.45	-	-	-
Mer009	0.06	0.06	-	-	-

last population of black-footed ferrets) would have increased allelic diversity in extant ferrets by 50% (Wisely and others, 2002).

Diversity and Structure in Captivity

Although Meeteetse animals were first captured in 1985, successful breeding was not achieved until 1987 (Clark, 1994). Of the 18 animals that survived in captivity, only 8–11 founders (unknown paternity of some wild-caught litters created some uncertainty as to the exact number) were initially represented in the pedigree; 20 years later, only 7 founders are represented in the extant population (Garell and others, 1998). The consequences of this bottleneck were measureable. Had five more of the original 18 ferrets bred successfully, genetic diversity of the extant population would have increased by 30% (fig. 2; Wisely and others, 2003). Once animal husbandry was understood and disease concerns were alleviated, the population quickly expanded, and the remaining genetic diversity was conserved (Wisely and others, 2003).

The dramatic loss of approximately 90% of the species' genetic diversity necessitated conservation of that which remained. Because all captive populations are susceptible to problems associated with small population size, including

inbreeding, inbreeding depression, and genetic drift (de Boer, 1994), management of the remaining genetic variation was a high priority (Ballou and Oakleaf, 1989). Various approaches have been used to maximize retention of genetic variability; for the black-footed ferret, the mean kinship strategy augmented with line breeding of underrepresented founders was recommended (Ballou and Oakleaf, 1989). Briefly, mean kinship strategy finds suitable breeding pairs that maximize the representation of the most underrepresented founders of the captive population. Over time, this strategy is predicted to maximally conserve genetic diversity. Empirically, it appears that this strategy has succeeded in adequately preserving genetic diversity. Founders' genes were more evenly represented in the captive population in 1999 than in the first generation of captive black-footed ferrets (fig. 1; Wisely and others, 2003), and even representation of founders maximally conserves genetic diversity in a pedigreed population. Likewise, a pedigree-based estimate of loss of heterozygosity was 12%, which meets the goal established by the Species Survival Plan of retaining 80% of the genetic diversity of the founding population for 25 years (Garell and others, 1998). Molecular-based estimates revealed no loss of allelic diversity; all alleles present in the founders were present in the extant population (Wisely and others, 2003).

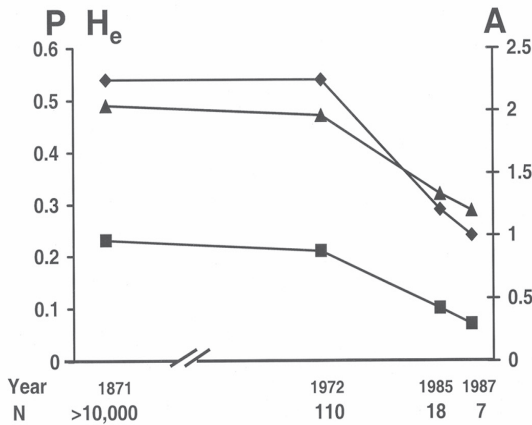


Figure 1. A timeline of genetic diversity in the black-footed ferret. A, the average number of alleles per locus (triangle); H_e , expected heterozygosity (diamond); and P, the proportion of polymorphic loci (square) were at their highest values in 1871. In 1972 only two populations remained, in Mellette County, South Dakota and Meeteetse, Wyoming. Note that although many populations throughout the Great Plains were extirpated, genetic diversity did not appreciably decrease. With the loss of the Mellette County population, substantial amounts of genetic diversity were lost. Only Meeteetse, Wyoming remained in 1982. Further loss of genetic diversity occurred due to a bottleneck in the last population from 1982 to 1987. From Wisely and others (2002). Reprinted with permission of Oxford University Press, Oxford, U.K.

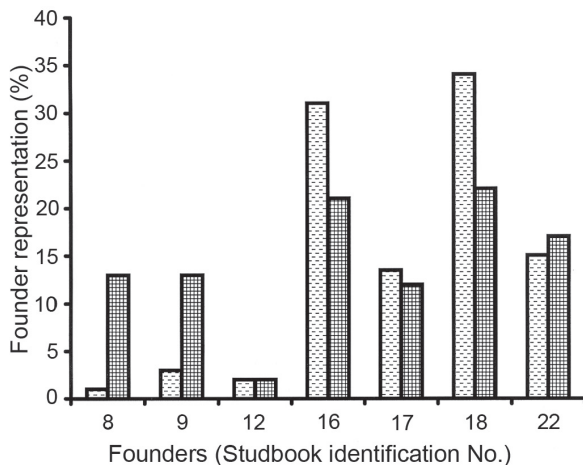


Figure 2. Founder representation in the first generation of captive breeding (i.e., all the direct descendants) (hatched bars), and in 1999, after 14 years of captive breeding (cross-hatched bars). Only founders with genes represented in the extant population are considered. From Wisely and others (2003). Reprinted with permission of Wiley-Liss, Hoboken, New Jersey.

Diversity and Structure of Reintroduced Populations

Once captive-born animals were released into the wild, further challenges faced the recovery program. A successful captive breeding reintroduction program involves substantive but reconcilable trade-offs. Demographic and genetic attributes affect the success of reintroduced populations (Jiménez and others, 1994; FitzSimmons and others, 1997), yet selection of animals for release removes them and their potentially unique genes from the captive breeding pool. This sets up a potential conflict between the goals of captive breeding and reintroduction (Earnhardt, 1999). Because of the tenuous nature of the early captive breeding program and the recognition that captive breeding would need to be maintained for many years, inbred animals and animals with a mean kinship >0.125 were designated for release (Ballou and Oakleaf, 1989). This strategy would maximize retention of genetic diversity in the captive population.

Inbreeding in 1991, estimated from pedigree analysis, was higher in released captive-bred animals ($F = 0.092$) than in animals retained in the captive population ($F = 0.052$; Russell and others, 1994) as expected by the designation criteria for animals retained versus released from the captive population. By 1999, overall inbreeding was higher (as would be expected in a small, closed population) but the difference between captive breeders and captive releases was negligible ($F = 0.12$ and 0.11 , respectively; Wisely and others, 2003). The gap between breeders and releases was closed because founder genes were more evenly represented in the 1999 than in the 1991 captive population (fig. 2), resulting in a panmictic population. Equal founder representation reduced the variance in mean kinship of individuals, which in turn decreased the difference in genetic composition between breeders and releases (Wisely and others, 2003).

As of 1999 no difference in genetic diversity had been detected between captive-reared releases and their wild descendants from Charles M. Russell National Wildlife Refuge, Montana and Conata Basin, South Dakota (table 2; Wisely and others, 2003). This finding suggests that initial releases and subsequent augmentation were sufficient to halt drift-induced losses in diversity. Small but statistically significant population differentiation ($F_{ST} = 0.09$, 95% CI = $0.04-0.13$) between wild descendants of two reintroduced populations suggested that even with augmentation of captive animals to the reintroduced population, these two populations had measurable genetic differences attributable to random differences in the founders of each reintroduction site (Wisely and others, 2003). Whether this statistically significant difference is also biologically significant is difficult to say (Hedrick, 1999). It is likely, however, that as populations grow and augmentation ceases, continuing genetic drift will decrease genetic diversity within populations and increase genetic distance among populations.

Table 2. Measures of genetic diversity, H_o , the observed heterozygosity, and H_e , the expected heterozygosity, for five groups of black-footed ferrets, and HWE P , the probability of heterozygote deficiencies (an indicator of inbreeding) within groups. H_e and H_o values were averaged over the seven microsatellite loci that were polymorphic in the historical Wyoming population. Each of the seven loci had two alleles per locus in each group of ferrets. Both captive breeders and captive releases showed evidence of inbreeding as predicted by pedigree-based methods. From Wisely and others (2003). Reprinted with permission of Wiley-Liss, Hoboken, New Jersey.

Group	n	H_o	$H_e \pm 2SE$	HWE P
Founders	7	0.40	0.33 ± 0.14	0.76
Captive breeders	29	0.32	0.41 ± 0.12	0.03
Captive releases	36	0.31	0.38 ± 0.14	0.01
Wild Montana	81	0.33	0.33 ± 0.14	0.47
Wild South Dakota	41	0.43	0.38 ± 0.12	0.87

Because wild-born animals were descended from animals with higher than average mean kinship and inbreeding (as calculated using the pedigree and estimated using microsatellites), it was predicted that the offspring would be inbred. In fact, this was not the case (table 2; Wisely and others, 2003). This result was surprising inasmuch as free ranging populations were smaller than the captive population, released animals were the descendants of over-represented individuals, and litter mates often were released together. A possible explanation for the lack of inbreeding in the wild populations is a behavioral response of inbreeding avoidance. Several researchers have proposed that closely related individuals avoid mating in such species as black-tailed prairie dogs (*Cynomys ludovicianus*; Hoogland, 1982), olive baboons (*Papio anubis*; Packer, 1979), and the marsupial genus *Antechinus* (Cockburn and others, 1985). Given that the reintroduced founding populations were small and that black-footed ferrets avoided close kin matings, survival and reproduction of founding populations may have been less than optimal as reintroduced individuals avoided breeding with one another and dispersed to find unrelated mates (Wisely and others, 2003).

The Future

The consequence of dramatic loss of genetic diversity in a species is unclear. Some taxa, such as felids, are highly susceptible to inbreeding depression, while other taxa appear unaffected (Ralls and Ballou, 1983; Lacy, 1997). Small, inbreeding populations have a higher rate of expression of deleterious alleles, which can lead to extinction when the forces of genetic drift are greater than natural selection. When selection exceeds drift, however, small, inbreeding populations can purge deleterious alleles, ultimately making them less

susceptible to inbreeding depression. To date, no physiological abnormalities have been linked to inbreeding depression in black-footed ferrets, although abnormalities exist (Howard and others, this volume). Indeed, fecundity of females (measured as kits surviving per litter) was virtually the same (3.1–3.3 kits per female) for animals observed in the historical populations of Mellette County, South Dakota (Hillman and Carpenter, 1980), and Meeteetse, Wyoming (Forrest and others, 1988), and the reintroduced population in Conata Basin, South Dakota (U.S. Department of Agriculture, 2000).

Without question the two biggest hurdles to recovery of this species are lack of suitable habitat for reintroduction and sylvatic plague (Conservation Breeding Specialist Group, 2003). Where ample, plague-free habitat exists, populations appear to flourish despite reduced genetic diversity. The dramatic loss of genetic diversity in this species should not discourage biologists from planning for recovery. With careful management of remaining genetic resources, this species will likely persist. Continued, vigilant conservation of genetic diversity in the captive population will be critical to the long-term success of this recovery effort. Likewise, genetic management of the reintroduced populations will be critical once populations become self-sustaining. Currently, only two populations are self-sustaining: Shirley Basin, Wyoming and Conata Basin, South Dakota. All other reintroduction sites rely on yearly augmentation to maintain their populations. Translocations for genetic augmentation may be necessary if reintroduced populations lose genetic diversity because of drift.

The dramatic loss of genetic diversity in this endangered species should serve as a reminder to conservation practitioners that proactive management of population structure (conserving as many individuals from as many geographic locations as possible) can have a profound effect on the conservation of genetic resources for a species. Furthermore, rapid breeding of as many founders as possible within the

first few generations of captive breeding will maximize the retention of the remaining genetic diversity and increase the likelihood of persistence into the future.

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