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Mortality of Siberian polecats and black-footed ferrets released onto prairie dog colonies

Dean E. Biggins,* Brian J. Miller, Louis R. Hanebury, and Roger A. Powell

United States Fish and Wildlife Service, National Ecology Research Center, 4512 McMurray Avenue, Fort Collins, CO 80525, USA (DEB, BJM, LRH)
Department of Biology, North Carolina State University, Raleigh, NC 27695-7617, USA (RAP)
Present address of DEB: United States Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, CO 80526-8118, USA (DEB)
Present address of BJM: Wind River Ranch, P.O. Box 27, Watrous, NM 87753, USA (BJM)
Present address of LRH: Western Area Power Administration, 2900th Avenue N, 6th floor, Billings, MT 59101, USA (LRH)

** Correspondent: dean_biggins@ugsg.gov*

Black-footed ferrets (*Mustela nigripes*) likely were extirpated from the wild in 1985–1986, and their repatriation depends on captive breeding and reintroduction. Postrelease survival of animals can be affected by behavioral changes induced by captivity. We released neutered Siberian polecats (*M. eversmanii*), close relatives of ferrets, in 1989–1990 on black-tailed prairie dog (*Cynomys ludovicianus*) colonies in Colorado and Wyoming initially to test rearing and reintroduction techniques. Captive-born polecats were reared in cages or cages plus outdoor pens, released from elevated cages or into burrows, and supplementally fed or not fed. We also translocated wild-born polecats from China in 1990 and released captive-born, cage-reared black-footed ferrets in 1991, the 1st such reintroduction of black-footed ferrets. We documented mortality for 55 of 92 radiotagged animals in these studies, mostly due to predation (46 cases). Coyotes (*Canis latrans*) killed 31 ferrets and polecats. Supplementally fed polecats survived longer than nonprovisioned polecats. With a model based on deaths per distance moved, survival was highest for wild-born polecats, followed by pen-experienced, then cage-reared groups. Indexes of abundance (from spotlight surveys) for several predators were correlated with mortality rates of polecats and ferrets due to those predators. Released black-footed ferrets had lower survival rates than their ancestral population in Wyoming, and lower survival than wild-born and translocated polecats, emphasizing the influence of captivity. Captive-born polecats lost body mass more rapidly postrelease than did captive-born ferrets. Differences in hunting efficiency and prey selection provide further evidence that these polecats and ferrets are not ecological equivalents in the strict sense.

Key words: captive breeding, *Cynomys*, ecological equivalent, ecological surrogate, *Mustela eversmanii*, *Mustela nigripes*, predation, reintroduction, survival, translocation

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Reintroduction, the intentional movement of captive-raised animals to reestablish populations within their former range (Beck et al. 1994), is an important technique in the array of strategies necessary for preservation of biodiversity. Yet, the captive environment can produce profound effects on the natural behavior and physiology of an animal. Relaxed natural selection (or artificial selection) and cultural transmission of behaviors during captivity can alter behavioral repertoires important to survival in the wild. These effects vary greatly between and within species and can manifest themselves in differential survival postrelease (Kleiman 1989). One review judged as successful only 16 of 145 attempts to reintroduce captive-born animals of various species (Beck et al. 1994). Because captive breeding and reintroduction are costly (Synder et al. 1996), the critical steps in the process should be investigated carefully. A stepwise process toward development of reintroduction methods can initially involve closely related species. For example, the Andean condor (*Vultur*

Fig. 1.—Adult male Siberian polecat (*Mustela eversmanii dauricus*) translocated from natural habitat in Inner Mongolia, China, and adult male black-footed ferret (*M. nigripes*).

gryphus) was used to test reintroduction techniques for the California condor (*Gymnogyps californianus*—Wallace 1989).

Black-footed ferrets (*Mustela nigripes*) were extirpated from the wild in 1985–1986, and their recovery remains dependent on reintroductions (United States Fish and Wildlife Service 1988), mostly from captive-born stock (but see Biggins et al. 2011a). Similar to the California condor, some types of investigations on black-footed ferrets (hereafter, ferrets) have been precluded because of their rarity and legally endangered status. Siberian polecats (*M. eversmanii*), closely related to ferrets (Fig. 1), have been substituted as investigational surrogates (Gaynor et al. 1997; Hill and Carpenter 1982; Martin et al. 1984; Mead et al. 1988; Powell et al. 1985; Williams et al. 1991). Laboratory evaluations demonstrated that rearing conditions affected development of predatory and antipredator behaviors in Siberian polecats (Biggins 2000; Miller et al. 1990a, 1990b). Ferrets and Siberian polecats (hereafter, polecats) have interbred and produced fertile offspring at the Wyoming captive-breeding facility during the 1980s, supporting morphological (Anderson et al. 1986) and genetic evidence of relatedness (O'Brien et al. 1989).

Procedures that seem intuitively fruitful for improving success of reintroductions include provisioning, acclimatization, and prerelease training (Beck et al. 1994). We conducted a preliminary evaluation of 5 different combinations of prerelease experience (rearing), acclimatization in postrelease retention cages, and postrelease provisioning (Table 1) by releasing and radiotracking 55 polecats during 1989–1990 (Biggins et al. 2011b) and monitoring rates and causes of mortality. In addition, we radiotracked 37 of the 1st ferrets released (in 1991) as a pilot test of techniques. Due to factors beyond our control, all ferrets were released using a single design, although the merits of comparative designs were debated (Biggins et al. 2006b; Miller et al. 1996). Releases of ferrets and polecats under similar conditions also enabled further evaluation of hypothesized ecological equivalence (Biggins et al. 2011b; Hoffmann and Pattie 1968) of the 2 species.

Materials and Methods

Study sites.—Polecats and ferrets were released at 3 sites (Table 1). Success of released polecats and ferrets could be related to the number of prairie dogs (*Cynomys* spp.) as prey and number of prairie dog burrows (escape cover) in their new habitat. We sampled the 2 polecat release sites and the ferret release site with strip transects to estimate prairie dog densities from density of active burrows (Biggins et al. 1993).

We released polecats near Veteran, Wyoming, on a 250-ha black-tailed prairie dog (*C. ludovicianus*) colony with an estimated 74 active burrows/ha and about 23 prairie dogs/ha. Nearby colonies were small and separated by >1 km. Other potential prey species were cottontail rabbits (*Sylvilagus*), kangaroo rats (*Dipodomys ordii*), deer mice (*Peromyscus maniculatus*), and pocket gophers (Geomyidae, *Geomys* or *Thomomys*). Wild polecats hunt ecologically similar prey in their Asian habitat (Stroganov 1962; Zheng et al. 1983). In 1989 about 30 coyotes (*Canis latrans*) were removed from the surrounding area (according to local rancher, G. Booth, pers. comm.). Sport hunters on several occasions chased and killed coyotes on and near the study area using dogs.

A 2nd release site for polecats was near Hasty, Colorado, a 250-ha black-tailed prairie dog colony with 34 active burrows/ha and about 11 prairie dogs/ha. Several other colonies (some of which were >1,000 ha) were within 2 km. Other prey species were similar to those at Veteran, but the geomyid present was the yellow-faced pocket gopher (*Cratogeomys castanops*). Hay meadows, other croplands, and a riparian

Table 1.—Number of released Siberian polecats (*Mustela eversmanii*) and black-footed ferrets (*M. nigripes*) monitored via radiotelemetry to assess cause-specific mortality rates.

				Rearing and release method				
			Rearing	Cage	Cage	Cage	Pen	Wild
			Release	Burrow	Burrow	Cage	Burrow	Burrow
Species	Site	Year	Provisioning	Unfed	Fed[a]	Fed	Fed	Fed
Polecat	Veteran, Wyoming	1989		6	7			
Polecat	Veteran, Wyoming	1990				8	18	3
Polecat	Hasty, Colorado	1990				6	5	2
Ferret	Shirley Basin, Wyoming	1991				37		

[a] Animals provided with supplemental food after release.

zone along the nearby Arkansas River created a varied mix of habitats. The only predator control at this site was by sport hunting.

We released ferrets in Shirley Basin, Wyoming, on a 660-ha white-tailed prairie dog (*Cynomys leucurus*) colony with 82.7 active burrows/ha and about 12 prairie dogs (Oakleaf et al. 1991). This colony was part of a complex with >20,000 ha of mapped colonies. Several other colonies were within 1 km of the release colony. Prior to release of the ferrets 66 coyotes and 63 badgers (*Taxidea taxus*) were removed from the Shirley Basin complex to monitor diseases and enhance ferret survival. Sport hunting of coyotes with dogs occurred on the study site.

Translocation.—In 1990 we translocated 5 wild-born polecats (*M. eversmanii dauricus*) from eastern Inner Mongolia, China. These animals were quarantined in cages in China for at least 1 month prior to shipment and quarantined for an additional 40–62 days in cages in the United States prior to release. We provided both live and dead prey items (prairie dogs and small mammals) while polecats were in quarantine cages.

Rearing.—Captive-born polecats were produced at the National Zoo Conservation and Research Center by animals obtained from the Moscow Zoo, Russia, which derived from lineages of unknown subspecies and origin. We cross-fostered captive-born polecats in 1990 between pen-reared and cage-reared groups (Table 1) to distribute related individuals across both treatments. Cage-reared ferrets and polecats were raised in 1.22 × 1.22-m cages with attached nest boxes and were fed commercial ferret ration and dead prairie dogs. We acclimated them to their release cages for 2 weeks at their release sites.

We initially raised pen-experienced polecats (Table 1) to 3.5 months of age in 2 × 3-m cages and then placed them into 2 pens (at the United States Army Pueblo Chemical Depot, Pueblo, Colorado, and at the National Zoo Conservation and Research Center), each having a seminatural enclosed prairie dog colony established in a 200-m^2 building filled with soil to a depth of 1.3 m. Pen-experienced polecats lived in burrows in these pens for 6–8 weeks prior to release. Their food was live black-tailed prairie dogs. Young animals stayed with their mothers until time of release.

Release.—Ferrets and polecats were fully grown when released in September–November and were mostly 4–6 months old (except 3 adult female polecats in the pen group that were released with their kits). We sterilized polecats at least 3 weeks before release (removal of oviducts or vasa deferentia and epididymides). We left ovaries and testes intact to minimize impact on behaviors (Kastner and Apfelbach 1987). We weighed polecats and ferrets before release and recaptured them periodically for reweighing and to assess general condition.

In 1989 we released polecats directly into burrows; 7 were provisioned and 6 were not (Table 1). In 1990–1991 we released wild-born or conditioned polecats and ferrets directly into burrows, but we released cage-reared polecats and ferrets from field cages similar to their rearing cages (Table 1). Their natal nest boxes were attached to release cages. After 10–14 days of on-site acclimation we opened a 12-cm-diameter plastic tube descending from each cage floor to the ground, allowing animals to leave. We provided dead prairie dogs in the cage for 10 days postrelease.

We released wild-born and pen-conditioned polecats directly into burrows in groups of 2–4 animals that had been housed together for at least 1 month prior to release. We supplemented each group with portions of prairie dog at the time and burrow of release and in other occupied burrows on days 3 and 8 postrelease (Table 1). Animal handling and monitoring procedures were approved by animal care and use committees at the National Zoo, Washington, D.C., and the United States Fish and Wildlife Service National Ecology Research Center, Fort Collins, Colorado. Research was done humanely and in accordance with guidelines of the American Society of Mammalogists that were later published (Gannon et al. 2007). Experimental rearing and releasing of ferrets was conducted under endangered species permit PRT-704930.

Radiotelemetry.—We monitored released ferrets and polecats (n = 92) via radiotelemetry (Table 1) using the D-2 transmitter described by Biggins et al. (2006a). We restrained animals physically (captive-born polecats) or immobilized them with ketamine hydrochloride (wild-born polecats and ferrets) for collaring. Duration of intensive monitoring by triangulation (Biggins et al. 2006a) varied from <1 day to 42 days, resulting in 765.4 radiodays of monitoring (1 radioday = 1 radiotagged animal monitored for 1 day). We estimated movements as cumulative straight-line distances between consecutive telemetric fixes, which usually were separated by <15 min when animals were above ground (Biggins et al. 1999). In addition, we used combinations of receivers and strip chart recorders to acquire nonlocational data on signal modulation and pulse interval (Biggins 2000); recorders were used when stations were not occupied by technicians and when animals were beyond reception range of the fixed stations.

Classification of mortality.—We determined causes for mortality of polecats and ferrets from evidence at kill sites (digging, tracks, scat, feathers, and fur) and necropsies of remains. Sources of predation were categorized as coyotes, American badgers, great horned owls (*Bubo virginianus*), diurnal raptors, and unidentified predators. Most other mortality was due to starvation, which included animals recovered and rehabilitated after they were too weak to hunt and an animal that became malnourished due to embedded porcupine quills in the head and mouth. We located badger-killed and starved polecats and ferrets from signals transmitted through the soil and dug vertical holes until the burrows and remains were intercepted. The 2 deaths that we could not attribute to predation or starvation were included in an analysis of overall mortality only.

Data analyses.—We used program MICROMORT (Heisey and Fuller 1985) in a competing risk analysis of survival and mortality, relating numbers of deaths to radiodays of monitoring. Daily survival rate during a time interval i is $\hat{s}_i$,

the probability that an animal alive at the beginning of a day will survive until the beginning of the next defined day (Heisey and Fuller 1985). Survival over an interval of L_i days is $\hat{S}_i = \hat{s}_i^L$. The method assumes a constant hazard rate to losses throughout the estimation interval, plausible if long time periods are subdivided into short periods. We used 2 intervals, release through day 3 postrelease and days 4–10 postrelease, as a starting point for most analyses. The method also assumes independence of each animal-day (1 individual animal monitored for 1 day). We derived rates of mortality solely from animals known to be dead; those rates, therefore, are minimum rates.

Much of the risk of predation for ferrets and polecats is associated with movement above ground. To assess the abilities of polecats to evade predators while engaging in high-risk activity we used mortality rates relative to cumulative aboveground movement. The procedure was analogous to using deaths per time, but in the survival analyses radiometers (the base measure was deaths per 100 m of movement) was substituted for radiodays of the time-based procedure. For this distance-based measure badger predation was not considered because it occurred below ground at polecat and ferret resting sites.

Likelihood ratio (LR) tests assisted in selection of the most-parsimonious nested submodel explaining significant variation in survival. Parenthetical chi-square (χ^2) values refer to likelihood ratio tests except when noted. The overriding goal was to investigate biological processes (i.e., to compare rearing methods, sexes, and sites) rather than to estimate accurately actual survival rates (Lebreton et al. 1992).

We counted nocturnal predators and small mammals while spotlighting from a vehicle at about 1 h after sunset and at 0000 h, using a 300,000–candle-power light. Preestablished 5.2-km routes traversed the experimental prairie dog colonies. Surveys at Shirley Basin and Veteran in 1989 occurred after most predator control was completed. Overall predator and prey sighting rates were compared among study sites using distribution-free methods (Kruskal–Wallis chi-square) in the MINITAB 8 statistical software package (Addison-Wesley Publishing Co., Reading, Massachusetts).

Risk of predation on polecats and ferrets can depend partly on their encounter rates with large predators. We compared sighting rates (numbers of predators per hour) with predator-specific mortality rates for polecats and ferrets at those sites (from the MICROMORT estimates), using linear regression analysis in MINITAB. Square root transformation of the predator sighting rate and mortality rate data resulted in improved normality and homoscedasticity of residuals.

Because of the unbalanced overall design (Table 1), we used different subsets of polecat data to optimize balance and sample size for each evaluation. We compared burrow releases with and without supplemental provisioning within the 1989 Veteran data set, using the time-based survival model. We compared the Hasty and Veteran sites within sexes and 2 rearing and release groups (cage–cage and pen–burrow). We assessed site effect with both time-based and distance-based estimates of mortality rate. To evaluate rearing methods we used a 1990 female-only subset with the cage–cage, pen–burrow, and wild groups (6 parameters), and both time and distance models. We used a subset of 1990 data to compare cage-reared and cage-released with pen-reared and burrow-released groups of captive-born polecats, comparing these groups within males at Veteran and within females at Hasty and Veteran, with time-based and distance-based estimates of mortality.

Starvation should have a delayed effect compared to predation, suggesting separate analyses of predation and starvation and further justifying separation of the 2 time periods. We characterized predation and starvation separately for ferrets, for polecats at both Hasty and Veteran, and for sexes of both species. We pooled polecat rearing and release groups into a large subset containing all captive-born animals but retained identity of the 2 sites.

We weighed animals to the nearest 10 g at the time of radiocollaring, before release, when they were recaptured for collar replacement or for inspections of overall condition, and when they were recaptured during spotlight surveys (Biggins et al. 1998). For a few deceased animals we weighed intact remains. We used multiple regression (in MINITAB) to assess effects of time, species, and sex on postrelease change in body mass expressed as a proportion of mass at the time of release. General models were reduced by stepwise removal of variables that appeared to have little influence ($P < 0.05$).

From data summarized by Forrest et al. (1988) we used MICROMORT to compare survival of the captive-born ferrets released at Shirley Basin, Wyoming, in 1991 to survival of radiotagged ferrets monitored in the wild population at Meeteetse, Wyoming. We contrasted a simple, 2-parameter general model (wild and captive) to a reduced model with pooled rearing categories. We made a similar comparison between captive-born ferrets and the wild-born polecats from China; both groups were translocated, unlike the Meeteetse ferrets.

Results

Radiotracking from fixed stations produced 5,662 estimates of location. We used additional nonlocational data (4,571 data lines) from stations occupied by technicians and automated equipment to help determine status (alive or dead) and timing of mortality for 55 deaths (Table 2). Overall survival rates of captive-born animals were highly variable among sites (Table 3).

Badgers ate their ferret and polecat kills. Radiocollars, bits of hair and skin, and sometimes the head were excavated from badger-enlarged prairie dog burrows at depths of 0.8–2.2 m. Two radios recovered from 2.2 m deep could be heard only a few meters away (laterally); thus, some badger kills might not have been found. Coyotes often did not eat the polecats or ferrets they killed but carried them from kill sites on the prairie dog colony to cache sites off the colony. Cache sites were holes dug by the coyotes, 10–30 cm deep, in which the

Table 2.—Number of deaths of radiotagged Siberian polecats (*Mustela eversmanii*) and black-footed ferrets (*M. nigripes*) due to various causes.

Species	Site	Cause of mortality				
		Coyote	Badger	Starvation	Other	All
Polecat	Veteran, Wyoming[a]	15	12	5	2[b]	34
Polecat	Hasty, Colorado	11	0	0	1[c]	12
Ferret	Shirley Basin, Wyoming	5	1	2	1[d]	9
Total		31	13	7	4	55

[a] 1989 and 1990 combined.
[b] Diurnal bird of prey (unknown species).
[c] Great horned owl.
[d] Golden eagle.

Table 3.—Overall estimates of maximum daily survival and minimum daily mortality for captive-born Siberian polecats (*Mustela eversmanii*) and black-footed ferrets (*M. nigripes*) released onto prairie dog colonies. Daily rates are calculated for the first 10 days postrelease.

Species	Site (Year)	Daily rates			
			Cause of mortality		
		Survival (*SD*)	Coyote	Badger	Other
Polecat	Veteran, Wyoming (1989–1990)	0.8867 (0.0180)	0.0486	0.0389	0.0259
Polecat	Hasty, Colorado (1990)	0.1589 (0.0913)	0.8411	0.0000	0.0000
Ferret	Shirley Basin, Wyoming (1991)	0.9764 (0.0078)	0.0131	0.0026	0.0079

mustelids were coiled and covered by soil and ground litter. Radiotagged polecats left in 3 cache sites at Veteran for 4, 6, and 9 days remained uneaten, after which we removed the polecat remains. Polecats killed by coyotes at Hasty were eaten, often on the prairie dog colony; remains were limited to head and radiocollar, but death was assumed due to coyotes and not badgers if remains were on the surface and were not accompanied by sign of badgers (digging or tracks). In several of these cases at Hasty we located polecat remains within 1.5 h of predation, as suggested by motion-sensitive transmitters, and saw coyotes retreating from the remains as we approached. A great horned owl caused the only known death of a wild-born polecat, and that was the only death in any of the groups due to an owl (the polecat was consumed). A captive-born polecat was killed by an unidentified diurnal raptor.

The 2 polecats that survived longest (about 5 days) at Hasty were wild-born. An adult female moved 1 km from the prairie dog colony and hunted in yellow-faced pocket gopher burrows for several days. Excavation of burrows in that area revealed pocket gopher remains (skin, feet, etc.) and uneaten supplemental food that we had left. A dead 510-g pocket gopher was recovered from a burrow 10 m from the last known location of the polecat. Two of the longest survivors (a pen-experienced polecat who lived 33.3 days and a wild-born polecat who survived 41.9 days) at Veteran also moved away from the prairie dog colony and occupied pocket gopher burrows, but the only prey known to have been killed was a cottontail.

The high density of predators at Hasty (Table 4) provided an opportunity to observe their reactions to the release cages containing polecats and associated food. Coyotes were observed within 100 m of the cages on several occasions, day and night. During the prerelease acclimation period a golden eagle (*Aquila chrysaetos*) was flushed from the ground within a few meters of an occupied cage.

Sighting rates for combined predators (Table 4) differed significantly among the 3 sites (Kruskal–Wallis $\chi^2_1 = 13.70$, $P = 0.001$). Alternative prey species (leporids and *D. ordii*) were not surveyed at Shirley Basin, but sighting rates for those species combined were significantly higher at Hasty than at Veteran (Kruskal–Wallis $\chi^2_1 = 13.52$, $P < 0.001$). Kangaroo rats were not known to have been killed by polecats during this study. Although a 10-fold higher density of leporids at Hasty might have provided the polecats with additional prey, it also could help explain the high density of coyotes at that site. Sighting rates for coyotes, badgers, and great horned owls were related to mortality rates of ferrets and polecats attributable to those 3 predators ($R^2 = 0.707$, $F_{1,7} = 16.90$, $P = 0.005$).

Effect of rearing and release methods.—For the test of supplemental provisioning done in 1989 the overall daily mortality rate ($1 - \hat{s}_i$) of the supplemented polecats (0.0924) was lower (LR $\chi^2_1 = 5.9$, $P = 0.015$) than the mortality rate for nonsupplemented polecats (0.3333). Moreover, supplemental provisioning seemed to reduce the rate of predation. Daily mortality rates due to predation also were lower (LR $\chi^2_1 = 4.7$, $P = 0.030$) for the supplemented group (0.1109) compared to the nonsupplemented group (0.4000).

Using the restricted subset of data with captive-born polecats of both sexes in 1990 (Table 1), site (Hasty or Veteran) was a significant covariate in both the time-based model (LR $\chi^2_4 = 43.0$, $P < 0.001$) and the distance-based model (LR $\chi^2_4 = 32.9$, $P < 0.001$) of survival rate (Fig. 2), with lower survival rates at the Hasty site than at the Veteran site. We therefore retained site as a covariate in the models to examine effect of rearing.

Using the subset of data with female polecats released in 1990, rearing and release appeared to affect time-based survival estimates (LR $\chi^2_4 = 14.1$, $P = 0.007$) and distance-based survival estimates (LR $\chi^2_4 = 23.9$, $P < 0.001$). Wild-born, translocated polecats consistently had the highest survival rates. Using males released at Hasty and females released at both sites to compare rearing methods for captive-born polecats (Fig. 2), general models were not different from reduced models for either time-based survival estimates (LR $\chi^2_3 = 4.7$, $P = 0.195$) or distance-based estimates (LR $\chi^2_3 = 3.7$, $P = 0.296$).

Pen-raised polecats practiced hunting and killing prairie dogs in captivity, but we found no evidence that they were able to kill free-ranging prairie dogs. Wild-born polecats made no attempt to kill live prairie dogs in captivity, although they ate prairie dog carcasses and they killed kangaroo rats and

Table 4.—Sighting rates for predators and alternative prey species along nocturnal survey routes.

Site (Year)	Surveys (*n*)	Index of abundance (sightings/h)				
		Coyote	Badger	Great horned owl	Hare and rabbit	Kangaroo rat
Veteran, Wyoming (1990)	10	0.45	0.45	0.00	2.87	0.91
Hasty, Colorado (1990)	9	1.65	0.37	0.73	31.74	1.47
Shirley Basin, Wyoming (1991)	18	0.18	0.26	0.00	Not counted	

other small mammals. We witnessed 1 aboveground encounter between a wild-born polecat (male) and a prairie dog, involving 3 brief bouts lasting 2–3 s each. Between encounters both animals assumed an alert position with all 4 feet on the ground. The first 2 bouts were initiated by the polecat, but the 3rd was initiated by the prairie dog. After the 3rd bout both animals retreated to separate burrows.

Because captive-born animals released at Hasty were killed by predators within 3 days, and because starvation at other sites occurred after 3 days postrelease, further analyses were conducted separately for the period 0–3 days postrelease and the period 4–10 days postrelease. The initial data set involved captive-born polecats and ferrets at all release sites. General statistical models of predation and starvation for the first 3 days had 6 parameters (2 sexes × 3 sites); the deletion of data from Hasty resulted in 4-parameter models for the 4- to 10-day period.

In all studies only 6 animals were classified as having starved. The 3 that actually died lost 33–40% of their body mass and survived 12–14 days after the last known meal. We have no evidence for differing starvation rates due to sex or to the confounded species and sites variable (sexes: LR χ^2_2 = 1.2, P = 0.549; species and sites: LR χ^2_2 = 0.8, P = 0.664). During the first 3 days postrelease losses to predation were

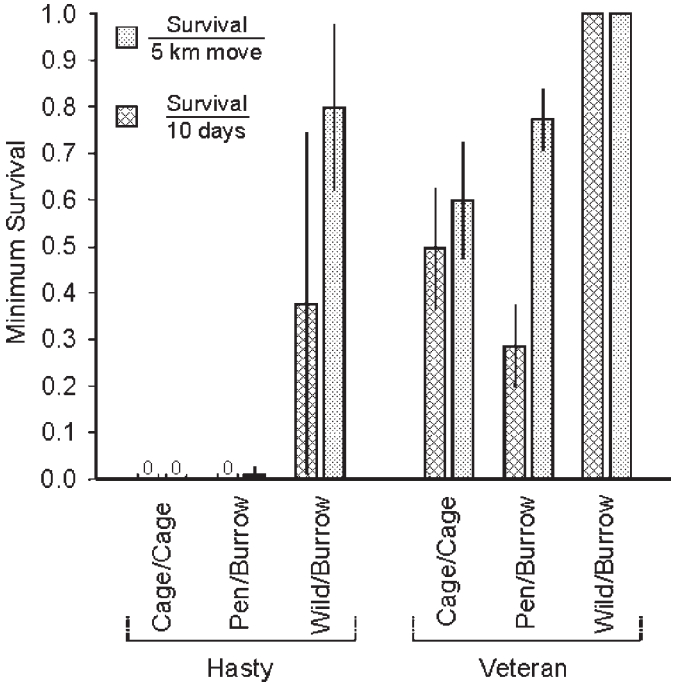

Fig. 2.—Time-based and movement-based probabilities of avoiding predation for Siberian polecats (*Mustela eversmanii*) with 3 rearing histories and 2 release methods. Bars indicate means ± 1 *SD*.

lower for males than for females (LR χ^2_3 = 8.0, P = 0.046) and for captive-born ferrets than for captive-born polecats at the 2 sites (LR χ^2_4 = 48.6, P < 0.001; Fig. 3), similar to the pattern for 4–10 days postrelease (sexes: LR χ^2_2 = 7.9, P = 0.019; species and sites: LR χ^2_2 = 24.5, P < 0.001).

In the general regression model of change in mass, the interaction of time and species was highly significant ($F_{1,42}$ = 18.36, P < 0.001), justifying segregation of species for further analyses. For captive-born polecats average masses at the time of release were 784 g for females and 1,382 g for males. Masses at release for translocated wild-born polecats were 693 g for females and 860 g for the lone male. We detected no effect of sex for polecats ($F_{1,16}$ = 2.15, P = 0.162) or the interaction between sex and time ($F_{1,16}$ = 1.22, P = 0.284) on change in mass (Fig. 4A). Days postrelease was a significant predictor in the 2-parameter model ($F_{1,18}$ = 52.51, P < 0.001); polecats typically lost 1.7% of their initial body mass per day postrelease.

Male and female ferrets responded differently (interaction of days postrelease and sex in a 4-parameter model: $F_{1,25}$ = 7.63, P = 0.011) in changes of mass over time (Fig. 4B), so we assessed the sexes separately. Male ferrets (average mass at release = 926 g) maintained their mass over time ($F_{1,12}$ = 0.55, P = 0.471). Although their changes in mass were less dramatic than those of polecats, female ferrets (average mass at release = 757 g) lost mass at a rate of 0.6% per day postrelease ($F_{1,13}$ = 8.72, P = 0.011).

The estimated 10-day survival for wild-born polecats (88%) was higher than for released ferrets (51%). The species were compared using a model that controlled for sex (LR χ^2_2 = 13.1, P < 0.001). The survival rate for released ferrets (49% for 1 month) was lower (LR χ^2_1 = 14.4, P < 0.001) than survival for free-ranging wild ferrets (93% for 1 month) at Meeteetse, Wyoming.

Discussion

In our studies the effect of predation was dramatic. At Hasty survival times were measured in hours, and all polecats were killed by predators. Even the released ferrets at Shirley Basin suffered a mortality rate of about 51% per month (extrapolated from the daily survival rate; Table 3). In contrast, the relatively low mortality rate of about 7% per month for free-ranging ferrets at Meeteetse (Forrest et al. 1988) suggest that released polecats and ferrets had antipredator defenses compromised by captive breeding and translocation. The extraordinary mortality rates for ferrets and polecats with presumably compromised skills underscore the tenet of Lima

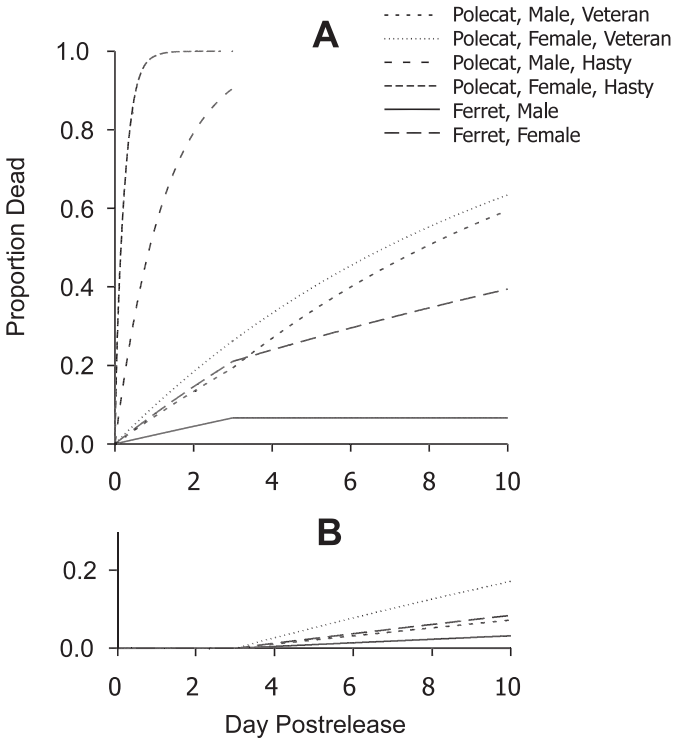

Fig. 3.—Models of A) predation and B) starvation for captive-born black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmanii*) spanning 10 days after release near Hasty, Colorado, and Veteran, Wyoming.

and Dill (1990:634) that observed predation rates [in wild populations of animals] may not be good indicators of potential risk because ''… antipredator behavior may be so effective that predators are rarely successful.''

Small mustelines can be common prey for larger predators (King and Powell 2007; Korpimaki and Norrdahl 1989a; Latham 1952; Lindström et al. 1995; Mulder 1990), and predation sometimes limits weasel populations (Craighead and Craighead 1956; Korpimaki and Norrdahl 1989a, 1989b; Powell 1973). Furthermore, numerous studies of mesopredator release have shown that large carnivores directly and indirectly affect small predators, and therefore the community structure (Bolger et al. 1991; Crabtree and Shelton 1999; Crooks and Soulé 1999; Estes et al. 1998; Henke and Bryant 1999; Palomares et al. 1995; Schoener and Spiller 1999; Soulé et al. 1988; Sovada et al. 1995; Vickery et al. 1992). Nonetheless, relatively little information exists concerning predation on nonreintroduced populations of ferrets (Forrest et al. 1988; Henderson et al. 1974; Sperry 1941) and polecats (Kydyrbaev 1988). In Kazakhstan food habits studies of predators demonstrated predation on polecats by 4 mammalian predators and 1 avian predator, but predators were not thought to influence polecat populations (Kydyrbaev 1988). Such dismissal of predation as being important has been the historical norm (Powell 1973). The correlation we detected between sighting rates for predators and mortality of ferrets and polecats suggests that attention be paid to densities of predators at future reintroduction sites for ferrets.

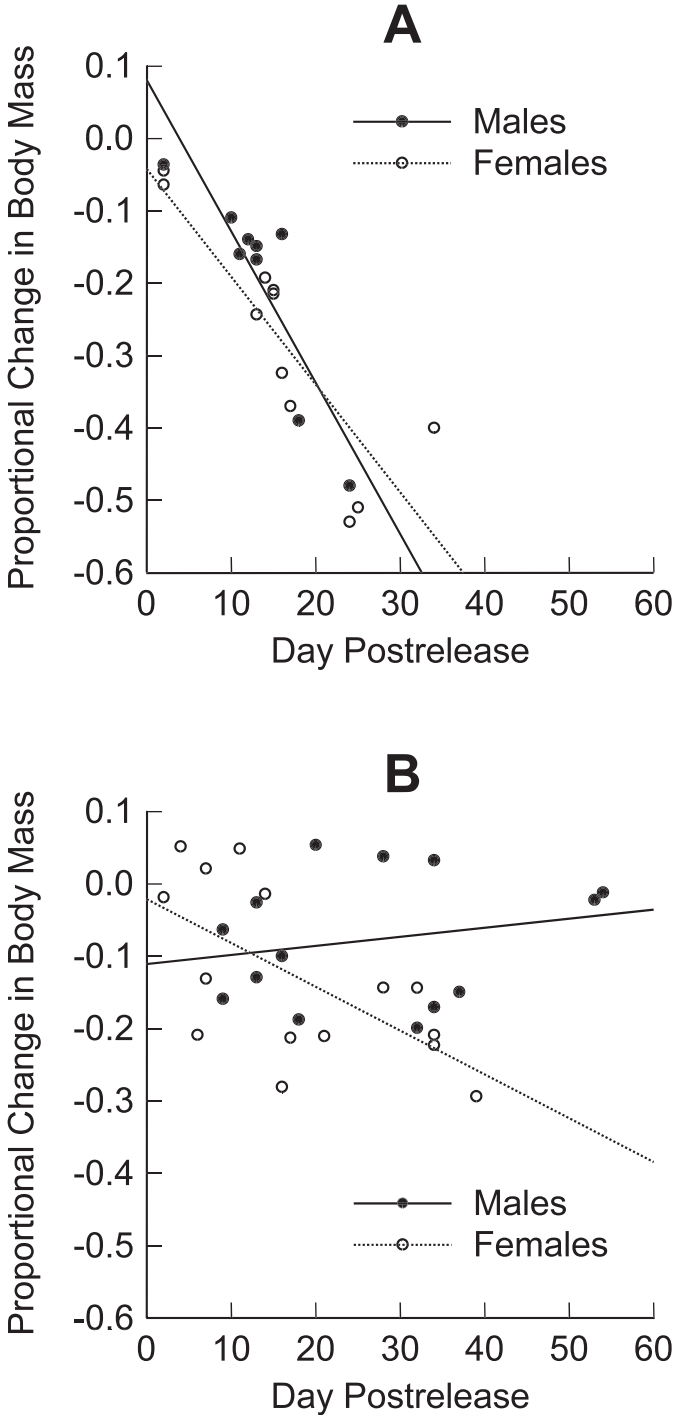

Fig. 4.—Change in body mass of A) Siberian polecats (*Mustela eversmanii*) and B) black-footed ferrets (*M. nigripes*) after release onto prairie dog colonies in Colorado and Wyoming (change expressed as a proportion of prerelease mass).

High density of prey (sciurids, murids, and leporids) and midsized predators at Hasty emphasizes a potential trade-off with high prey abundance for ferrets and polecats. With high prey density energetic requirements are met more easily, their reproductive success can be high, and their risk of predation can be low due to short periods spent hunting above ground. High prey density, however, can result in high densities of

other predators. By killing prey nearly as large as themselves and by occupying the retreats of those prey, ferrets and polecats, like weasels (Craighead and Craighead 1956; Korpimaki and Norrdahl 1989a, 1989b), become vulnerable to opportunistic attack by mesopredators hunting prey. Midsized predators such as badgers and coyotes likely kill ferrets and polecats as incidental prey or to eliminate competitors rather than as a primary food source; these predators are unlikely to respond directly to ferret or polecat densities. The hazard rate for ferrets and polecats appears determined by the density of prey shared with other mesopredators rather than their own densities.

Predation rates of ferrets in our study decreased over time. As animals with deficient skills were culled, those remaining had better skills on average. Also, skills and knowledge should improve as animals learn about their new environment. Despite polecats and ferrets not being released at the same sites, the low predator abundance at Shirley Basin suggests that site differences explain at least part of the lower mortality rate of ferrets compared to polecats.

Much of the overall difference in the comparison of survival for 3 categories of rearing (Fig. 2) appeared to be due to the relatively high survival for wild-born polecats, but the intermediate survival of the pen-reared group using the distance-based model suggested pen experience is beneficial. Despite the confounding of site and species, the higher survival for wild-born polecats compared to captive-born ferrets is noteworthy because polecats were released onto ferret habitat. The higher monthly survival rate for wild-born ferrets at Meeteetse, Wyoming (Forrest et al. 1988), compared to that of captive-born ferrets released at Shirley Basin provides further evidence for effects of captivity.

Differences in survival of pen-experienced and wild-born polecats, both subjected to the stresses of translocation, imply that the effects of captivity (Biggins 2000) might not be overcome fully by giving animals experience in a more natural environment. Transferring kits (age 3.5 months) to pens presumably exposed them to natural stimuli (e.g., burrows as home sites and prairie dogs as food) during sensitive periods for learning. Other potential benefits include opportunity for habituation to nonthreatening stimuli (Shalter 1984), reduced habituation to humans, and refinement of hunting and killing skills (Biggins 2000).

The cage-release acclimation and provisioning method seemed to prolong polecat survival. During the first 2 weeks supplemental feeding should have satisfied all energetic needs of the polecats (Powell et al. 1985). While using cages the animals had unlimited access to water, but free water probably was not available after release. Thus, part of the postrelease change in body mass could have been due to change in water balance. Because rates of mortality per kilometer moved tended to be higher for cage-released animals than for pen-reared and burrow-released animals, advantages of postrelease support appear superficial. Reduced activity encouraged by release cages might reduce risk of predation temporarily, but longer term success will require aboveground forays to hunt, gain familiarity with the habitat, and interact with conspecifics. Although burrow releases with supplemental provisioning have not been tested on ferrets, they might benefit less than the polecats in our study did because ferrets seemed more skilled at procuring their own food on prairie dog colonies. Advantages of supplemental feeding of polecats in burrows were offset by the attractiveness of such burrows to badgers (D. E. Biggins, pers. obs.), a phenomenon that is likely to have increased the predation rate for the provisioned group and could pose a similar problem if in-burrow provisioning were used for ferrets.

We detected an intersexual difference in change of mass after ferrets were released. Perhaps the male ferrets in 1991, which were about 22% larger than the females of that cohort, could kill prairie dogs more easily than the females could. Equal degradation of killing skills resulting from captivity thus might have greater impact on females than on males. Wild and captive ferrets routinely kill prairie dogs (Campbell et al. 1987; Vargas 1994), but injuries we have noticed in pen-raised ferrets and in free-ranging wild ferrets suggest that adult prairie dogs, about equal in size to these polecats and ferrets, are not easy prey. Also, young male ferrets tend to reach adult size later than females (Vargas 1994) and are 95% of adult mass at 126 days of age, compared to females which are 99% of adult mass at that age. Thus, the pattern of slow gain in mass after their release (Fig. 4) might be expected.

Although predation was identified more often than starvation as the cause of death for polecats and ferrets, the relative importance of the 2 causes cannot be distinguished using our data. First, risk of predation could increase as animals become malnourished and increase their own hunting activity or become weak. Second, these risks are competing but involve different time spans. An animal that would starve within 2 weeks is subjected to 14 days of predation risk.

The greater tendency for starvation and significantly greater loss of body mass of captive-born polecats compared to ferrets suggests that polecats were not well adapted to killing prairie dogs as prey. Pocket gophers, presumably killed by polecats during these studies, are ecologically similar to zokors (*Eospalax* spp.) found in Asia. Polecats were observed to dig into zokor burrows in Inner Mongolia (D. E. Biggins, pers. obs.), and zokors (*Eospalax fontanierii*) are important polecat prey in Qinghai Province, China (Zheng et al. 1983). Sciurid rodents, murid rodents, and ochotonids are well represented in the diet of the polecats over their Eurasian range (Denisov 1984; Gorbunov 1983; Kydyrbaev 1988; Peshkov 1954; Stroganov 1962; Zheng et al. 1983). Polecats might be prey or habitat generalists (Clark 1989; Erickson 1973; Forrest et al. 1985, 1988), in the sense of killing a wide variety of prey over their large Asian range, but specialize locally or regionally, and apparently cannot adapt quickly to all prey species killed by other mustelines of similar size.

The term ecological equivalent (Hoffmann and Pattie 1968) needs concise definition when applied to ferrets and polecats. Polecats are ecological equivalents of ferrets in the general sense of different taxa that perform similar ecological roles in different geographical areas (Lincoln et al. 1998), but they fail

to meet criteria of other definitions. First, they are not unrelated or distantly related species (Lincoln et al. 1998) that reflect convergent evolution. Second, evidence from our study suggests differences that might prevent either form from successfully occupying habitat of the other, thus failing to support a definition that emphasizes substitutability of species (Lincoln et al. 1998) and making polecats imperfect ecological surrogates for ferrets (Biggins et al. 2011b). Nevertheless, polecats used in our study provided the 1st evidence regarding high predation rates on captive-reared and released animals of this (*putorius*) subgenus of *Mustela*. They also gave preliminary evidence of the utility of prerelease experience and a 1st assessment of the advantages and disadvantages of on-site acclimatization and postrelease provisioning as tools used in reintroductions of these taxa.

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Literature Cited

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.

Beck, B. B., L. G. Rapaport, M. R. S. Price, and A. C. Wilson. 1994. Reintroduction of captive-born animals. Pp. 265–286 in Creative conservation: interactive management of wild and captive animals (P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, eds.). Chapman and Hall, London, United Kingdom.

Biggins, D. E. 2000. Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*): conservation and evolutionary implications. Ph.D. dissertation, Colorado State University, Fort Collins.

Biggins, D. E., J. L. Godbey, L. R. Hanebury, B. Luce, 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.

Biggins, D. E., J. L. Godbey, B. M. Horton, and T. M. Livieri. 2011a. Movements and survival of black-footed ferrets associated with an experimental translocation in South Dakota. Journal of Mammalogy 92:742–750.

Biggins, D. E., J. L. Godbey, B. J. Miller, and L. R. Hanebury. 2006a. Radio-telemetry for black-footed ferret research and monitoring. Pp. 175–189 in Recovery of the black-footed ferret—progress and continuing challenges (J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, eds.). United States Geological Survey Scientific Investigations Report 2005—5293.

Biggins, D. E., L. R. Hanebury, B. J. Miller, and R. A. Powell. 2011b. Black-footed ferrets and Siberian polecats as ecological surrogates and ecological equivalents. Journal of Mammalogy 92:710–720.

Biggins, D. E., B. J. Miller, T. W. Clark, and R. P. Reading. 2006b. Restoration of an endangered species: the black-footed ferret. Pp. 581–585 in Principles of conservation biology (M. J. Groom, G. K. Meffe, and C. R. Carroll, eds.). 3rd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

Biggins, D. E., et al. 1993. A technique for evaluating black-footed ferret habitat. Pp. 73–87 in Management of prairie dog complexes for the reintroduction of the black-footed ferret (J. L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, eds.). United States Fish and Wildlife Service Biological Report 1993—13.

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.

Bolger, D. T., A. C. Alberts, and M. E. Soulé. 1991. Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. American Naturalist 105: 467–478.

Campbell, T. M., III, 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.

Clark, T. W. 1989. Conservation biology of the black-footed ferret (*Mustela nigripes*). Wildlife Preservation Trust Special Scientific Report 3, EcoHealth Alliance, New York.

Crabtree, R. L., and J. W. Shelton. 1999. Coyotes and canid coexistence in Yellowstone. Pp. 127–164 in Carnivores in ecosystems: the Yellowstone experience (T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Karieva, eds.). Yale University Press, New Haven, Connecticut.

Craighead, J. J., and F. C. Craighead, Jr. 1956. Hawks, owls and wildlife. Stackpole Co. and Wildlife Management Institute, Washington, D.C.

Crooks, K., and M. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Denisov, E. I. 1984. Study of the biology of steppe polecats in the period of raising the young. Izvestiya Sibirskogo Otdeleniya, Akademii Nauk SSSR, Seriya Biologicheskikh Nauk. 15:89–93.

Erickson, R. C. 1973. Some black-footed ferret research needs. Pp. 153–164 in Proceedings of the black-footed ferret and prairie dog workshop (R. L. Linder and C. N. Hillman, eds.). South Dakota State University, Brookings.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476.

FORREST, S. C., ET AL. 1988. Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985. Journal of Mammalogy 69:261–273.

FORREST, S. C., T. W. CLARK, L. RICHARDSON, D. E. BIGGINS, AND T. M. CAMPBELL III. 1985. Life history characteristics of the genus *Mustela* with special reference to the black-footed ferret, *Mustela nigripes*. Pp. 23.1–23.17 in Black-footed ferret workshop proceedings, 18–19 September 1984 (S. H. Anderson and D. B. Inkley, eds.). Wyoming Game and Fish Department, Cheyenne.

GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

GAYNOR, J. S., J. WIMSATT, C. MALLINCKRODT, AND D. BIGGINS. 1997. A comparison of sevoflurane and isoflurane for short-term anesthesia in polecats. Journal of Zoo and Wildlife Medicine 28:274–279.

GORBUNOV, A. V. 1983. Variations of mustelid populations in northwest Turkmenia and the southern Ustyurt. Izvestiya Akademii Nauk Turkmenskoi SSR 4:51–56.

HEISEY, D. M., AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using radio-telemetry data. Journal of Wildlife Management 49:668–674.

HENDERSON, R. R., P. F. SPRINGER, AND R. ADRIAN. 1974. The black-footed ferret in South Dakota. Technical Bulletin Number 4, South Dakota Department of Game, Fish and Parks, Pierre, South Dakota.

HENKE, S. E., AND F. C. BRYANT. 1999. Effects of coyote removal on the faunal community in western Texas. Journal of Wildlife Management 63:1066–1081.

HILL, E. F., AND J. W. CARPENTER. 1982. Responses of Siberian ferrets to secondary zinc phosphide poisoning. Journal of Wildlife Management 46:678–685.

HOFFMANN, R. S., AND D. L. PATTIE. 1968. A guide to Montana mammals. University of Montana, Missoula.

KASTNER, D., AND R. APFELBACH. 1987. Effects of cyproterone acetate on mating behavior, testicular morphology, testosterone level, and body temperature in male ferrets in comparison with normal and castrated males. Hormone Research 25:178–184.

KING, C. M., AND R. A. POWELL. 2007. The natural history of weasels and stoats: ecology, behavior, and management. 2nd ed. Oxford University Press, New York.

KLEIMAN, D. G. 1989. Reintroduction of captive mammals for conservation. BioScience 39:152–160.

KORPIMAKI, E., AND K. NORRDAHL. 1989a. Avian predation on mustelids in Europe 1: occurrence and effects on body size variation and life traits. Oikos 55:205–215.

KORPIMAKI, E., AND K. NORRDAHL. 1989b. Avian predation on mustelids in Europe 2: impact on small mustelid and microtine dynamics—a hypothesis. Oikos 55:273–276.

KYDYRBAEV, KH. K. 1988. Ecology of the Siberian polecat in Kazakhstan. Academy of Sciences of Kazakh SSR, Transactions of the Institute of Zoology 44:56–58.

LATHAM, R. M. 1952. The fox as a factor in the control of weasel populations. Journal of Wildlife Management 16:516–517.

LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

LINCOLN, R., G. BOXSHALL, AND P. CLARK. 1998. A dictionary of ecology, evolution, and systematics. 2nd ed. Cambridge University Press, Cambridge, United Kingdom.

LINDSTRÖM, E. R., S. M. BRAINERD, J. O. HELLDIN, AND K. OVERSKAUG. 1995. Pine marten–red fox interactions: a case of intraguild predation. Annales Zoologici Fennici 32:123–130.

MARTIN, S. J., M. H. SCHROEDER, AND H. TIETJEN. 1984. Burrow plugging by prairie dogs in response to Siberian polecats. Great Basin Naturalist 44:447–449.

MEAD, R. A., M. M. JOSEPH, AND S. NEIRINCKX. 1988. Optimal dose of human chorionic gonadotropin for inducing ovulation in the ferret. Zoo Biology 7:263–267.

MILLER, B., ET AL. 1990a. Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*) I: locating prey. Journal of Ethology 8:89–94.

MILLER, B., ET AL. 1990b. Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*) II: predator avoidance. Journal of Ethology 8:95–104.

MILLER, B., R. READING, AND S. FORREST. 1996. Prairie night—black-footed ferrets and the recovery of endangered species. Smithsonian Press, Washington, D.C.

MULDER, J. L. 1990. The stoat *Mustela erminea* in the Dutch dune region, its local extinction, and a possible cause: the arrival of the fox *Vulpes vulpes*. Lutra 33:1–21.

OAKLEAF, B., E. THORNE, B. LUCE, AND B. WILLIAMS. 1991. Black-footed ferret reintroduction. Annual Report. Wyoming Game and Fish Department, Cheyenne.

O'BRIEN, S. J., J. S. MARTENSON, M. A. EICHELBERGER, E. T. THORNE, AND F. WRIGHT. 1989. Biochemical genetic variation and molecular systematics of the black-footed ferret, *Mustela nigripes*. Pp. 21–33 in Conservation biology and the black-footed ferret (U. S. Seal, E. T. Thorne, M. A. Bogan, and S. H. Anderson, eds.). Yale University Press, New Haven, Connecticut.

PALOMARES, F., P. GAONA, P. FERRERAS, AND M. DELIBES. 1995. Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. Conservation Biology 9:295–305.

PESHKOV, B. I. 1954. Data on the population of predators in the southeastern Transbaikal. Izvestiya Irkutskogo Gosudarstvennogo Na Uchno-Issledovatel 'Skoga Protivochumnogo Instituta Sibiri 12:217–223.

POWELL, R. A. 1973. A model for raptor predation on weasels. Journal of Mammalogy 54:259–263.

POWELL, R. A., T. W. CLARK, L. RICHARDSON, AND S. W. FORREST. 1985. Black-footed ferret (*Mustela nigripes*) energy expenditure and prey requirements. Biological Conservation 33:1–15.

SCHOENER, T. W., AND D. A. SPILLER. 1999. Indirect effects in an experimentally staged invasion by a major predator. American Naturalist 153:347–358.

SHALTER, M. D. 1984. Predator–prey behavior and habituation. Pp. 349–391 in Habituation, sensitization, and behavior (H. V. S. Peeke and L. Petrinovich, eds.). Academic Press, New York.

SOULÉ, M. E., E. T. BOLGER, A. C. ALBERTS, J. WRIGHT, M. SORICE, AND S. HILL. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75–92.

SOVADA, M. A., A. B. SARGEANT, AND J. W. GRIER. 1995. Differential effects of coyotes and red foxes on duck nest success. Journal of Wildlife Management 59:1–9.

SPERRY, C. G. 1941. Food habits of the coyote. United States Fish and Wildlife Service, Wildlife Research Bulletin 4:1–70.

Stroganov, S. U. 1962. Carnivorous mammals of Siberia. Translation: Israel Program for Scientific Translations, Jerusalem, 1969. United States Department of Commerce, Clearinghouse for Federal Scientific and Technical Information, Springfield, Virginia.

United States Fish and Wildlife Service. 1988. Black-footed ferret recovery plan. United States Fish and Wildlife Service, Denver, Colorado.

Vargas, A. 1994. Ontogeny of the endangered black-footed ferret (*Mustela nigripes*) and effects of captive upbringing on predatory behavior and post-release survival. Ph.D. dissertation, University of Wyoming, Laramie.

Vickery, P. D., M. L. Hunter, Jr., and S. M. Melvin. 1992. Effects of habitat area on the distribution of grassland birds in Maine. Conservation Biology 8:1087–1097.

Wallace, M. 1989. Andean condor experimental releases to enhance California condor recovery. Endangered Species Update 6:1–4.

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 (*M. eversmanni*) with *Yersinia pestis*. Journal of Wildlife Diseases 27:441–445.

Zheng, S., J. Zeng, and R. Cui. 1983. On ecology and energy dynamics of masked polecat (*Mustela eversmanni*) in Haibei Qinghai Province. Acta Theriologica Sinica 3:35–46.

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