

Morphological changes to black-footed ferrets (*Mustela nigripes*) resulting from captivity

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Abstract: Captive breeding of endangered species carries risks associated with small population size and domestication. The black-footed ferret (*Mustela nigripes*) was among the first endangered species bred in captivity. We documented morphological changes to the species after >10 years of captive breeding. We measured 9 dental or cranial traits on 109 skulls; 85 specimens were collected prior to captivity and 24 specimens were of captive-born animals. Skulls of captive animals were 5–6% smaller than skulls from precaptive animals and were 3–10% smaller than skulls of animals collected near the founding population, suggesting that changes occurred in captivity rather than from sample bias in the founders of the captive population. Skull size did not correlate with inbreeding coefficients of captive animals, eliminating the possibility that black-footed ferrets were smaller because of the effects of inbreeding depression or overdominance. Although reintroduced animals were smaller than historical animals, we recommended no alterations to the current management because intentional selection for body size might further reduce genetic variation in a genetically impoverished species. We hypothesize that reintroduced individuals will return to historical body sizes rapidly, owing either to release of environmental stresses or to natural selection for larger size.

Résumé : L'élevage en captivité d'espèces menacées comporte des risques reliés aux petites populations et à la domestication. Le putois d'Amérique (*Mustela nigripes*) est l'une des premières espèces menacées à avoir été élevée en captivité. Nous avons étudié les changements morphologiques chez cette espèce après >10 ans d'élevage en captivité. Nous avons mesuré 9 caractéristiques dentaires ou caractéristiques crâniennes sur 109 crânes, dont 85 avaient été récoltés avant la période de captivité et les 24 autres provenaient d'animaux nés en captivité. Les crânes des putois en captivité étaient de 5 à 6 % plus petits que ceux prélevés chez des animaux capturés avant la période de captivité et de 3 à 10 % plus petits que ceux des animaux capturés dans le voisinage de la population fondatrice, ce qui semble indiquer que les changements se sont produits pendant la captivité et ne sont pas des artefacts dus à des erreurs d'échantillonnage des fondateurs de la population en captivité. Il n'y a pas de corrélation entre la taille du crâne et les coefficients de consanguinité chez les animaux en captivité, ce qui élimine la possibilité que les putois aient été plus petits à cause des effets de la détérioration due à la consanguinité ou à la surdominance. Bien que les putois réintroduits se soient avérés plus petits que les animaux d'origine, nous avons recommandé de ne faire aucune modification aux procédures d'aménagement en usage dans le moment parce que la sélection volontaire d'animaux de plus grande taille réduirait encore davantage la variation génétique chez cette espèce déjà appauvrie. Nous croyons que les animaux réintroduits reviendront à la taille d'origine, ou bien parce qu'ils ne seront plus soumis au stress environnemental, ou alors parce qu'ils auront subi la pression de sélection qui favorise une taille plus grande.

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Introduction

Captive propagation is a common last-resort measure to avoid extinction of animal taxa. In the captive setting, conservationists can reduce predation, avoid or treat disease, improve nutrition, and facilitate reproduction and care for neonates (Olney et al. 1994). However, captivity tends to cause phenotypic changes first described by Darwin (1859). With or without deliberate selection, these changes include increased thresholds to behavioral disturbance, relaxed selection for traits required for survival in the wild, and altered morphol-

ogy and reproductive rates (Frankham et al. 1986). Although they may be adaptive in and their frequency may be increased by the captive environment, these traits generally are not adaptive in the wild (Frankham et al. 1986). Therefore, the evolution of such traits in captivity is a concern where reintroduction to the wild is a goal (Lacy 1994). Although the theory of intentional and unintentional selection is well understood and documented for domesticated species (Frankham 1995; Jackson and Diamond 1996; Kruska 1996), no study has quantified morphological changes in endangered terrestrial vertebrates maintained in captivity.

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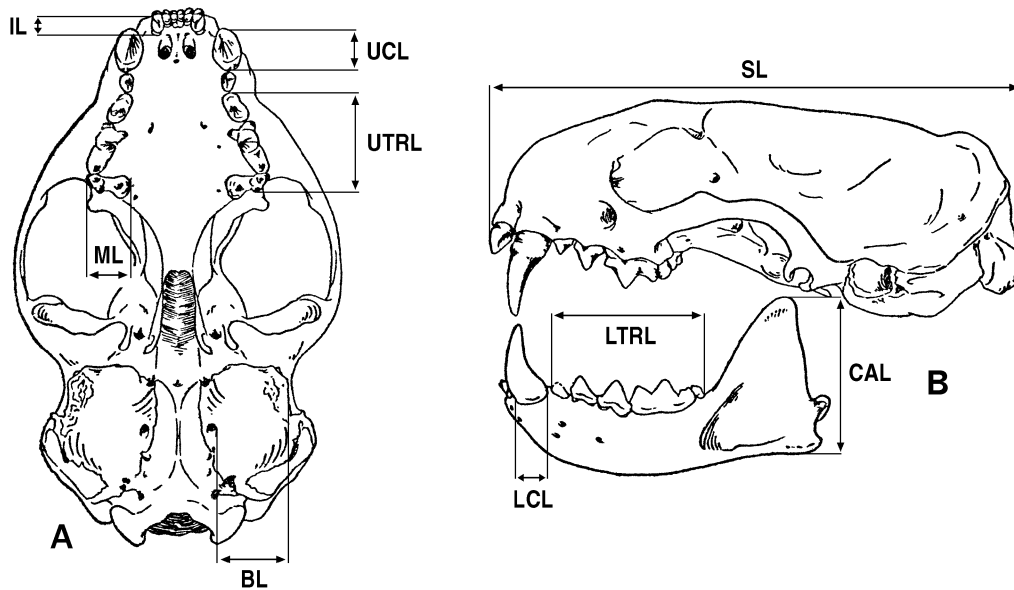
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Fig. 1. Black-footed ferret (*Mustela nigripes*) skull showing metric characters used in our study of morphology. IL, maxillary lateral incisor anteroposterior length; UCL, maxillary canine anteroposterior length; UTRL, maxillary tooth row length from the anterior border of the canine at the alveolus to the posterior border of M^1 at the alveolus; ML, anteroposterior length of M^1 ; BL, length from the external auditory meatus to the distal auditory bullae; LCL, mandibular canine anteroposterior length; LTRL, mandibular tooth row length from the anterior border of P_2 at the alveolus to the posterior border of M_1 at the alveolus; CAL, length of the coronoid process tip to the angular process tip; SL, length of skull from the tip of the premaxilla to the end of the occipital condyles. CPL, labiolingual length of the condyloid process, is not shown. (A) Ventral view of skull. (B) Lateral view of skull and mandible. Based on figure from Anderson et al. (1986).



The endangered black-footed ferret (*Mustela nigripes*) was taken into captivity from the last wild population in Meeteetse, Wyoming, between 1985 and 1986. Of 18 original members of the captive population, 7 bred, and over 3000 animals have descended from those matings (Garell et al. 1998). The demographic goal of captive breeding was a rapid increase in population size; the genetic goal was to retain remaining genetic variability by equalizing founder representation (Ballou and Oakleaf 1989). Mates were chosen so as to minimize variation in mean kinship, and as recommended by Frankham et al. (1986), phenotypic outliers were not culled from the population. Today, black-footed ferrets have been in captivity for approximately 6.5 generations (Wisely et al. 2002), and their descendants occur in six wild populations across the original range of the species in Montana, South Dakota, Wyoming, Colorado, Utah, Arizona, and Mexico. Here, we describe differences between morphological features of black-footed ferrets before versus during captivity, using craniometric and dental characters.

Materials and methods

Sample collection and measurement

We measured 9 morphological characters on the skulls of 109 black-footed ferrets (66 males and 43 females) from the following five mammal collections (Appendix A): Denver Museum of Nature and Science (DMNH); National Museum of Natural History (USNM); Field Museum of Natural History, Chicago (FMNH); University of Kansas Natural History Museum (KU); and U.S. Fish and Wildlife Service (nonaccessioned specimens now in the USNM). We categorized specimens as either precaptive ($n = 85$) or captive ($n =$

24). We made one additional measurement, total skull length, on a subset ($n = 41$) of precaptive museum specimens and on a larger sample of captive animals ($n = 33$).

Nine morphological measurements were made by J.J.O. for a study of fluctuating asymmetry. A 10th measurement, skull length, was also made by J.J.O. to increase the ease of interpretation of the results. The 10 skull and dental characters (Fig. 1) were measured with a digital caliper to the nearest 0.01 mm. All characters except skull length were bilateral and measurements were repeated on each side four times in succession. Skull length measurements were repeated twice and averaged. Variance associated with measurement error was <1% of the variance among individuals. Because measurements were made in succession, we likely underestimated measurement error. We calculated a left–right mean $((\text{right} + \text{left})/2)$ of each pair of bilateral measurements, then averaged the four repeated measures. We excluded characters from the analysis if the structure was missing or damaged.

The median collection year was 1918 (range 1862–1977) for precaptive animals and 1993 (range 1987–2000) for captive animals. We measured only animals with fully erupted adult teeth and closed cranial sutures. Permanent teeth fully erupt in black-footed ferrets at 84 days of age; females reach 95% of adult weight at age 100 days and males do at 120 days (Vargas and Anderson 1996). The mean age of captive specimens we measured was 1.3 years (range 0.5–2.3 years). Specimens from museum collections (all precaptive animals) were mature in terms of skeletal growth, but otherwise of undetermined age. Population studies of black-footed ferrets before 1985 were limited, but suggested that adults >3 years old were uncommon (Forrest et al.

Table 1. Mean \pm SE (mm) and n of 10 character measures in black-footed ferret (*Mustela nigripes*) specimens.

Character	Male		Female		<i>F</i> , <i>P</i>
	Precaptive	Captive	Precaptive	Captive	
IL	2.56 \pm 0.02, 50	2.43 \pm 0.03, 10	2.38 \pm 0.02, 26	2.28 \pm 0.03, 14	20.6, < 0.001*
UCL	4.43 \pm 0.03, 52	4.09 \pm 0.07, 9	4.02 \pm 0.07, 28	3.70 \pm 0.05, 14	48.4, < 0.001*
UTRL	13.10 \pm 0.05, 54	13.31 \pm 0.12, 10	12.46 \pm 0.07, 27	12.49 \pm 0.10, 14	1.6, 0.21
ML	5.69 \pm 0.03, 55	5.64 \pm 0.08, 10	5.45 \pm 0.05, 26	5.35 \pm 0.07, 14	1.4, 0.23
BL	10.02 \pm 0.08, 44	9.55 \pm 0.17, 9	9.30 \pm 0.10, 26	9.19 \pm 0.13, 14	5.6, 0.02
LCL	4.45 \pm 0.03, 51	4.21 \pm 0.06, 10	4.09 \pm 0.04, 29	3.83 \pm 0.05, 14	26.6, < 0.001*
LTRL	19.00 \pm 0.10, 47	18.40 \pm 0.22, 9	17.73 \pm 0.14, 25	17.12 \pm 0.20, 12	12.5, 0.001*
CAL	21.05 \pm 0.12, 47	19.29 \pm 0.27, 10	19.48 \pm 0.16, 28	17.77 \pm 0.26, 14	74.0, < 0.001*
CPL	11.77 \pm 0.10, 52	11.09 \pm 0.22, 10	10.86 \pm 0.13, 28	10.02 \pm 0.19, 14	21.0, < 0.001*
SL	68.37 \pm 0.41, 23	66.22 \pm 0.51, 13	64.06 \pm 0.43, 18	61.81 \pm 0.41, 20	25.5, < 0.001*

Note: Characters are as follows: IL, maxillary lateral incisor anteroposterior length; UCL, maxillary canine anteroposterior length; UTRL, maxillary tooth row length from the anterior border of the canine at the alveolus to the posterior border of M¹ at the alveolus; ML, anteroposterior length of M¹; BL, length from the external auditory meatus to the distal auditory bullae; LCL, mandibular canine anteroposterior length; LTRL, mandibular tooth row length from the anterior border of P₂ at the alveolus to the posterior border of M₁ at the alveolus; CAL, length of the coronoid process tip to the angular process tip; CPL, labiolingual length of the condyloid process; SL, length of skull from the tip of the premaxilla to the end of the occipital condyles. *F* statistics and *P* values are for the effect of the treatment group, captive or precaptive, on two group univariate ANOVAs. For each character, the overall model and the treatment group, male or female, were highly significant ($P < 0.001$). We found no significant interaction effect.

*Significant *P* values after a sequential Bonferroni adjustment (Rice 1989) corrected for experimentwise error.

Table 2. Eigenvalues, percent variance explained, and principal component (PC) loadings on original variables for PC1 and PC2 for male and female black-footed ferrets.

Character	Male		Female	
	PC1	PC2	PC1	PC2
Eigenvalue	2.03	0.21	2.15	0.34
Variance explained	74%	8%	74%	12%
IL	-0.07	0.00	-0.04	-0.07
UCL	-0.13	-0.02	-0.08	0.07
UTRL	-0.20	0.34	-0.10	-0.26
ML	-0.12	0.14	-0.08	-0.10
BL	-0.23	0.13	-0.19	-0.49
LCL	-0.10	-0.09	-0.07	-0.04
LTRL	-0.49	0.68	-0.36	-0.68
CAL	-0.67	-0.61	-0.78	0.45
CPL	-0.41	-0.07	-0.44	0.05

Note: Refer to Table 1 for character abbreviations.

1988). Although captive specimens >2.3 years old were available for measurement, older captive animals were senescent individuals whose teeth and palates were damaged by periodontal disease; therefore, they did not have consistently measurable traits for the first 9 characters. More individuals were available for the measure of total skull length because the trait was not affected by the age of the animal.

Ideally, to avoid unintentional bias in our measurements, information regarding the source population of each specimen should have been withheld from the observer. Older museum specimens, however, were clearly distinguishable from newly prepared specimens and therefore it was impossible to conceal the source. However, because the intent of this study was to measure fluctuating asymmetry, not to determine differences in body size, we believe that unintentional bias was not a factor in this study.

Statistical analysis

To maximize our sample size, we initially compared captive

and precaptive skulls using multiple univariate two-group ANOVAs with gender and captivity status (captive or precaptive) as treatment groups. We did not use a multivariate ANOVA because this method eliminates individuals with missing measures (resulting from missing or damaged characters). We initially tested for normality with a Kolmogorov–Smirnov test (Zar 1984). We corrected for experimentwise error with a sequential Bonferroni adjustment (Rice 1989).

Anderson et al. (1986) observed north–south clinal variation in skull size of precaptive black-footed ferrets. We used a posteriori principal component analysis (PCA) to compare skull size in different geographic groups with the captive population, to compare skull shape between captive and precaptive groups, and to visualize data. We calculated principal components (PC) loadings with a covariance, rather than a correlation matrix, because PCs 1 and 2 explained 10–16% more variance in the nine original variables when we used a covariance matrix. Furthermore, covariance is the preferred statistic when character measures are reasonably commensurable (Stevens 1992).

To determine whether skull size differed among captive and free-ranging animals from different geographic areas, we analyzed PC1 using ANOVA. We divided precaptive specimens into four geographic groups according to Anderson et al. (1986): Montana and North Dakota (MT, ND); Wyoming, South Dakota, and Nebraska (WY, SD, NB); Colorado and Kansas (CO, KS); and New Mexico, Arizona, and Texas (NM, AZ, TX). These four geographic classes and animals classified as captive constituted the treatment group. The NM, AZ, TX group was excluded from analyses of females, because $n = 1$. If the ANOVA test was significant, we used Tukey's honestly significant difference (HSD) to identify pairwise differences between groups (Zar 1984). Males and females were analyzed separately. To determine whether skull shape differed significantly between captive and precaptive animals, we conducted separate ANOVAs for males and females using PC2.

PC scores were not normally distributed; therefore, we used both the Kruskal–Wallis one-way (ANOVA) by ranks

Table 3. Mean \pm SD (mm) of female and male specimens collected from four geographic areas with clinal variation and specimens of captive animals.

Character	MT, ND	NB, SD, WY	CO, KS	AZ, NM, TX	Captive
Female	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 10	<i>n</i> = 1	<i>n</i> = 11
IL	2.32 \pm 0.09	2.42 \pm 0.03	2.37 \pm 0.12	2.46	2.29 \pm 0.08
UCL	4.00 \pm 0.10	3.89 \pm 0.15	3.98 \pm 0.21	4.02	3.71 \pm 0.10
UTRL	12.64 \pm 0.22	12.74 \pm 0.15	12.25 \pm 0.34	12.27	12.57 \pm 0.44
ML	5.49 \pm 0.43	5.68 \pm 0.16	5.34 \pm 0.27	5.16	5.38 \pm 0.15
BL	9.02 \pm 0.61	9.94 \pm 0.21	9.03 \pm 0.52	9.52	9.23 \pm 0.27
LCL	4.07 \pm 0.13	4.00 \pm 0.12	4.10 \pm 0.22	4.08	3.86 \pm 0.12
LTRL	17.32 \pm 0.87	18.35 \pm 0.24	17.49 \pm 0.61	17.77	17.12 \pm 0.55
CAL	19.52 \pm 0.65	20.30 \pm 1.05	18.82 \pm 0.99	19.02	17.77 \pm 0.34
CPL	10.95 \pm 0.39	11.48 \pm 0.48	10.44 \pm 0.63	10.45	10.07 \pm 0.32
Male	<i>n</i> = 4	<i>n</i> = 5	<i>n</i> = 18	<i>n</i> = 4	<i>n</i> = 6
IL	2.59 \pm 0.08	2.59 \pm 0.15	2.56 \pm 0.12	2.60 \pm 0.11	2.37 \pm 0.11
UCL	4.58 \pm 0.28	4.40 \pm 0.15	4.39 \pm 0.23	4.48 \pm 0.18	4.07 \pm 0.25
UTRL	13.31 \pm 0.23	13.12 \pm 0.38	13.01 \pm 0.46	13.17 \pm 0.27	13.02 \pm 0.45
ML	6.05 \pm 0.24	5.84 \pm 0.31	5.62 \pm 0.21	5.73 \pm 0.37	5.57 \pm 0.20
BL	9.75 \pm 0.68	9.86 \pm 0.66	9.99 \pm 0.39	10.56 \pm 0.26	9.58 \pm 0.41
LCL	4.46 \pm 0.17	4.49 \pm 0.05	4.52 \pm 0.21	4.48 \pm 0.27	4.11 \pm 0.31
LTRL	19.40 \pm 0.29	19.10 \pm 0.74	18.90 \pm 0.88	19.11 \pm 0.11	18.21 \pm 0.68
CAL	21.17 \pm 0.63	21.32 \pm 0.92	20.91 \pm 0.78	20.92 \pm 0.29	21.01 \pm 0.73
CPL	11.92 \pm 0.81	12.14 \pm 0.79	11.66 \pm 0.64	11.53 \pm 0.48	11.75 \pm 0.67

Note: Refer to Table 1 for character abbreviations. MT, Montana; ND, North Dakota; NB, Nebraska; SD, South Dakota; WY, Wyoming; CO, Colorado; KS, Kansas; AZ, Arizona; NM, New Mexico; and TX, Texas.

test and a parametric one-way ANOVA for all statistical tests that used PCs as dependent variables (Zar 1984). We inferred statistical significance where $P < 0.05$, unless otherwise noted. We reported only the results of the parametric ANOVA because inferences of significance from parametric and nonparametric tests were concordant in all cases.

Because captive black-footed ferrets were managed using a studbook, pedigrees for all captive-born animals were known. We calculated inbreeding coefficients for all captive specimens using the computer program SPARKS (Single Population Analysis and Records Keeping, v. 1.0; ISIS 1991). We tested for a significant association between total skull length, an individual's inbreeding coefficient, and year born, using ANOVA with gender and year as groups, and inbreeding as a covariate.

Results

All univariate ANOVAs performed on the original variables were significant for each of the 10 morphological characters. For all morphological characters, males were larger than females and in 7 of 10 skull measurements, precaptive black-footed ferrets were significantly larger than those of captive ferrets (Table 1). No interaction term between gender and captivity status was significant.

For both males and females, the greatest PC1 loadings (>0.40) were negatively correlated with original variables (Table 2). Given this trend, we interpreted PC1 as being correlated with overall skull size. PC2 explained less of the overall variance (8% for males and 12% for females). The greatest PC loadings were both positive and negative. We interpreted PC2 as being correlated with overall skull shape.

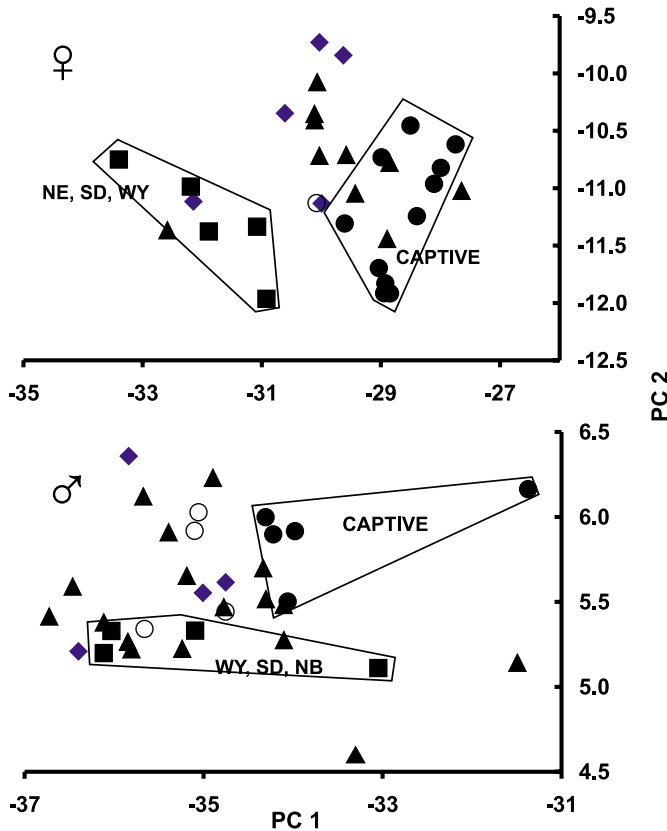
PC1 and PC2 combined explained 81–86% of the variance in analyses of male and female data (Table 2). ANOVAs

testing for differences in PC1 scores among latitudinal groups and captive animals were significant ($F_{[1,35]} = 5.3$, $P = 0.027$ for males and $F_{[1,30]} = 17.0$, $P < 0.001$ for females). Tukey's HSD revealed that captive female and male specimens were significantly smaller than animals from MT, ND and WY, SD, NB groups (Table 3, Fig. 2). Captive male specimens had a significantly different skull shape (PC2) than precaptive males ($F_{[1,36]} = 11.7$, $P = 0.002$). We found no difference in skull shape in females ($F_{[1,30]} = 3.5$, $P = 0.07$). We found no significant relationship between total skull length and inbreeding coefficient ($F_{[1,27]} = 0.52$, $P = 0.48$) or year born ($F_{[1,27]} = 0.43$, $P = 0.52$). Gender explained most of the variance ($F_{[1,27]} = 36.1$, $P < 0.001$).

Discussion

All morphological characters except bullae width and total skull length represented trophic structures of the skull, structures directly involved in prey capture, handling, and mastication. Trophic structures are highly evolved and differentiated among mustelid species (Butler 1946), and trophic morphology varies intraspecifically in other *Mustela* (Ralls and Harvey 1985). We, too, found intraspecific variation in black-footed ferret trophic structures as well as measurable differences between precaptive and captive specimens. Mandible measurements of captive black-footed ferrets averaged 5% smaller for males and 6% smaller for females than the average over the entire historic distribution of the species. Mandibles of captive males were 3% smaller and of captive females were 10% smaller than those of pre-bottleneck ferrets from Wyoming. Shape of the skull appeared to change as well. A significant difference was found in PC2 scores between captive and precaptive males. Results of the univariate ANOVAs on the original variables confirm that

Fig. 2. Data from the four geographic groups and captive specimens of female and male black-footed ferrets graphed on two-dimensional PC space. ●, captive specimens; ○, Arizona – New Mexico – Texas; ▲, Colorado–Kansas; ■, Nebraska – Wyoming – South Dakota; ◆, Montana – North Dakota. Polygons enclose individuals from the captive population and the Nebraska – Wyoming – South Dakota population.



whereas most cranial features became smaller in captivity, UTRL, ML, and BL did not change (Table 1, Fig. 1) resulting in ferrets with a different shape.

How did black-footed ferrets become smaller? Several explanations are possible. First, the animals at Meeteetse could have been atypical of (smaller than) the species generally. The primary environmental difference between Meeteetse and the areas from which most pre-bottleneck specimens came, at least as related to the anterior skull, is prey species. Black-footed ferrets are obligate predators of prairie dogs (*Cynomys* spp., Vargas and Anderson 1998). The white-tailed prairie dog (*Cynomys leucurus*), the species in Meeteetse, is smaller bodied than the black-tailed prairie dog (*Cynomys ludovicianus*) east of the Rocky Mountain front. This difference in prey size might seem capable of selection for animals with smaller feeding structures, but Anderson et al. (1986) found no differences in cranial size of black-footed ferret based on the species of prairie dog with which they were sympatric. This hypothesis is, therefore, an unlikely explanation for why ferrets today are smaller.

Second, reduced heterozygosity and increased inbreeding of black-footed ferrets resulting from many generations of captive breeding could have reduced body size through the general mechanisms that affect heterozygosity-mediated development. Multilocus heterozygosity was positively correlated with horn

or antler size in bighorn sheep (*Ovis canadensis*, FitzSimmons et al. 1995) and white-tailed deer (*Odocoileus virginianus*, Scribner et al. 1989). We found no correlation, however, between pedigree-based inbreeding coefficients and skull size, suggesting that the reduced genetic diversity of captive-bred black-footed ferrets was not associated with decreased body size.

Alternatively, the captive environment could have influenced the observed change in morphology in two ways. Changes could have been due to environmental factors that decrease body condition, but have no heritable basis, such as poor nutrition or high parasite loads. We would, however, expect to see a reduction in fecundity if these environmental stresses had limited the body size of ferrets. Prior to their extirpation from Meeteetse, female black-footed ferrets whelped and raised 3.2 ± 0.1 (SE) kits per litter (Forrest et al. 1988), which is similar to the 4.3 ± 0.9 kits per litter whelped by 1- to 3-year-old animals in captivity. Although these data are not directly comparable, it appears that there has not been a substantial change in fecundity associated with captivity. It therefore seems unlikely that environmental stress in captivity caused the decrease in body size in black-footed ferrets.

Finally, selection imposed by captivity and captive breeding could have caused smaller animals to produce more offspring or could have led to increased survival of those offspring. The observed morphological change in ferrets is consistent with changes associated with unintentional selection commonly seen in captive animals. Such changes include shortened facial features (Zeuner 1963), decreased brain size (Kruska 1996), and smaller body size (Frankham et al. 1986). These changes would have had to occur in very few generations with strong selective forces and in spite of efforts to minimize such forces. This seems plausible, however, given that selection intensity in captivity can be very strong. For example, Flesness and Cronquist-Jones (1987) estimated selection intensity to be 10–20 times greater for captive tigers (*Panthera tigris altaica*) than for an idealized free-ranging population, creating ample opportunity for rapid morphological change. Body size is an overwhelmingly integrative attribute (Clutton-Brock and Harvey 1983), responding to a wide range of genetic and environmental factors. Selection for body size is similarly complex, involving trade-offs between energetic costs, reproductive output, foraging efficiency, and interactions with other community members. Within species, body size tends to be large in seasonal environments, on islands, and for predators where prey are large. For example, skull size of ermine (*Mustela erminea*) was correlated with precipitation, latitude, and prey size (Ralls and Harvey 1985; Eger 1990), suggesting that prey size may be a selective force responsible for variation in predator skull size (King 1989). However, the ecological and evolutionary significance of clinal variation in skull size for black-footed ferrets is less clear. Black-tailed prairie dogs are larger at the northern and southern ends of their distribution, but smaller at middle latitudes (Pizzimenti 1975). Prey size, therefore, does not explain the clinal variation in size of black-footed ferrets. The characteristic long, slender shape of mustelines places serious constraints on thermoregulation (King 1989) and may exert selective pressure on the body size of black-footed ferrets at different latitudes.

The consequences of releasing small ferrets at latitudes that

once had animals as much as 10% larger are unknown. Currently, survival of reintroduced ferrets is greatly inflated by intensive management of disease, predators, and prey. Reproductive rates of ferrets, however, appear unaffected both in captivity and at the South Dakota reintroduction site (3.1 ± 0.2 kits whelped per female, USDA Forest Service 2000). If the change in skull size is not heritable, the first generation of wild-born animals should return to precaptive skull sizes and potential reductions in fitness be ameliorated. If the change in body size is heritable, natural selection could effect rapid evolutionary change. On the other hand, if the small body size is the result of bottleneck-induced losses of genetic variability, the restoration of larger body sizes could require many generations. We recommend against curtailing the reproduction of especially small captive breeders. For captive populations with limited genetic variability like black-footed ferrets (founder $N = 7$, founder genome equivalent = 4.1, Garell et al. 1998), culling outliers could substantially reduce variability (Frankham et al. 1986). In the wild, ontogenic influences or selection for large individuals will likely reverse this morphological change in black-footed ferrets quickly.

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Appendix A

List of catalogued museum specimens and non-accessioned specimens.

Catalogued specimens: DMNH 8277, DMNH 5199, DMNH 5792, DMNH 3644, DMNH 2371, DMNH 2248, DMNH 2247, DMNH 2024, DMNH 1987, DMNH 1883, DMNH 1684, DMNH 1558, DMNH 1208, DMNH 257, DMNH 1559, KU 121795, KU 1487, KU 10177, KU 134415, KU 14411, KU 7146, KU 11077, FMNH 25622, FMNH 8207, USNM 188455, USNM 188456, USNM 155475, USNM 188457, USNM 188458, USNM 224450, USNM 013113, USNM 188453, USNM 083992, USNM 232400, USNM 243820, USNM 234971, USNM 234972,

USNM 243819, USNM 234973, USNM 243818, USNM 234970, USNM A14580, USNM 243909, USNM 243910, USNM 209150, USNM 201945, USNM 251453, USNM 228789, USNM 287321, USNM 243799, USNM 349713, USNM 243990, USNM 285877, USNM 289498, USNM 349715, USNM 168741, USNM 349716, USNM 065061, USNM A34977, USNM 245641, USNM 211513, USNM 180719, USNM 019263, USNM 019262, USNM A35088, USNM 019294, USNM 019295, USNM 241014, USNM A35011, USNM 188454, USNM 083993, USNM 083994, USNM 110772, USNM 188450, USNM 188451, USNM 188452, USNM 015470, USNM 012299, USNM 015471, USNM 022537, USNM 022538, USNM 025358, USNM 022539, USNM 247073, USNM 234118, USNM 228233.

Non-accessioned specimens: SB2953, SB1633, SB2588, SB1722, 95W9597, 97M043, 93W6732, 93W6861, SB2682, 95W8742, SB2447, 92W9223, 99W9223, SB1153, SB1416, SB1435, FWS002, 97W1193, 94W8298, SB1576, SB1336, SB2178, 181019.