DISSERTATION

PREDATION ON BLACK-FOOTED FERRETS (*MUSTELA NIGRIPES*) AND SIBERIAN POLECATS (*M. EVERSMANNII*): CONSERVATION AND EVOLUTIONARY IMPLICATIONS

Submitted by

Dean E. Biggins

Biology Department

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2000

COLORADO STATE UNIVERSITY

March 1, 2000

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DEAN E. BIGGINS ENTITLED "PREDATION ON BLACK-FOOTED FERRETS (*MUSTELA NIGRIPES*) AND SIBERIAN POLECATS (*M. EVERSMANNII*): CONSERVATION AND EVOLUTIONARY IMPLICATIONS" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Adviser

Department Head

ABSTRACT OF DISSERTATION

PREDATION ON BLACK-FOOTED FERRETS (*MUSTELA NIGRIPES*) AND SIBERIAN POLECATS (*M. EVERSMANNII*): CONSERVATION AND EVOLUTIONARY IMPLICATIONS

These studies were part of a conservation effort to develop efficient methods to reestablish free-ranging populations of endangered black-footed ferrets (Mustela nigripes) from a captive population. Behaviors critical to survival in the wild may be altered during generations of captivity. We conducted arena trials with four generations of captive-bred Siberian polecats (Mustela eversmannii), mustelids closely related to black-footed ferrets, and with a small sample of ferrets. Changes in the polecats' exploration of a novel arena and reaction to a predator model implied increased boldness through successive generations in captivity, which could increase predation rates on released animals. Releases of reproductively sterilized polecats in 1989-90 and the first release of black-footed ferrets in 1991 underscored the importance of predation; 46 of 92 radio-tagged ferrets and polecats were killed by predators. Quasi-natural rearing environments seemed to counteract some effects of captivity. Survival was highest for translocated wild-born polecats, followed by polecats reared in outdoor pens and in indoor cages respectively. Wild-caught polecats translocated from China had higher survival rates than captive-reared ferrets released onto native habitat, suggesting strong effects of captivity. Survival was10-fold higher for pen-reared ferrets than for cage-reared ferrets at several release sites from 1992-1995.

To reduce risk of predation, small mammals commonly avoid moonlight, but ferrets and polecats were most active during bright moonlight. The apparently canalized circadian activity pattern of ferrets may help them avoid diurnal raptors and their important canid predator, the coyote (Canis latrans). In arena trials with simulated attacks by a stuffed owl, pre-attack latency of departure from shelter was shorter than was post-attack latency of departure for polecats, but not for ferrets. Compared to ferrets, polecats may rely more on risk assessment for decisions regarding timing of activity, induced by a temporally and spatially variable environment. In particular, plague (caused by Yersinia pestis) in Asia historically caused large fluctuations in populations of rodents, which may have favored prey-switching in polecats, increasing the complexity of their foraging/predator avoidance tradeoffs. The introduction of plague to western North America raises concerns regarding the highly specialized black-footed ferrets and their highly social prairie dog prey.

Dean Edwin Biggins
Biology Department
Colorado State University
Fort Collins, CO 80523
Summer 2000

ACKNOWLEDGMENTS

Paramount among these tributes is gratitude to my immediate family. Ferrets and polecats have been a focus of my attention for as long as Jason and Laura can remember. I am grateful for Denise's direct assistance in portions of the research, for her support during over 15 years of field and laboratory work, and her understanding regarding my status as life-long student.

I greatly appreciate the flexibility and patience of my advisor, Bruce Wunder, for enduring 10 years of annoyances imposed by my "non-traditional student" status. A former member of my graduate committee, Philip Lehner, influenced the experimental design, particularly for the laboratory research, through his verbal reminders and formalized model (Lehner, 1998) emphasizing consideration of all variables that can influence behavior. Roger Powell provided invaluable suggestions regarding mustelid ecology throughout the extended history of my work with black-footed ferrets (including studies done prior to this dissertation), and I appreciate his long-term friendship and encouragement. The varied perspectives on ferrets and prairie dogs provided by the expertise of Bill Andelt and Jim Detling helped me maintain a broader focus on the multitude of interacting factors affecting the prairie dog community. Special thanks are due to Brian Miller and Lou Hanebury for their direct participation in several of these studies, for many years of camaraderie during studies of ferrets and other fauna, and for assistance in ways too numerous to mention.

Funding for this project came from the Midcontinent Ecological Science Center (U. S. Fish and Wildlife Service and U. S. Geological Survey), Smithsonian Institution,

Loudon Area Ferret Fanciers, Friends of the National Zoo, National Fish and Wildlife Foundation, Bureau of Land Management, Chevron USA, the Legacy Program of the U.S. Department of Defense, Region 6 of the U.S. Fish and Wildlife Service, U.S. Forest Service, Montana Department of Fish, Wildlife and Parks, National Fish and Wildlife Foundation, National Park Service, South Dakota Department of Game, Fish and Parks, U.S. Air Force, U.S. Army, Wildlife Preservation Trust International, and Wyoming Game and Fish Department. I am especially grateful to Wildlife Preservation Trust International for long-term support of this conservation effort.

The black-footed ferret reintroductions that produced data for this report would not have been possible without tremendous teamwork and devotion of many individuals, including S. H. Anderson, B. Bessken, D. M. Christopherson, A. Dood, D. M. Garell, D. R. Gober, J. Godbey, J. J. Grensten, H. J. Harju, D. R. Kwiatkowski, M. E. Jennings, J. M. Lockhart, B. Luce, M. Lucero, M. R. Matchett, P. M. McDonald, P. Marinari, J. Montoya, R. J. Oakleaf, J. L. Oldemeyer, W. Perry, G. E. Plumb, B. D. Rosenlund, J. P. Roybal, L. R. Shanks, T. S. Smith, R. Stoneburg, E. T. Thorne, A. Vargas, E. S. Williams, and J. L. Wright. I thank Project Lighthawk, whose volunteer pilots and aircraft transported ferrets from zoos to preconditioning facilities and subsequently to remote reintroduction sites. I am deeply indebted to the zoos participating in the ferret recovery program (Cheyenne Mountain, Henry Doorly, Louisville, Metro Toronto, National, Phoenix), who produced about one-half of the ferrets that were reintroduced. I particularly thank the dedicated ferret caretakers at those institutions as well as caretakers

at the Wyoming Game and Fish Department's Sybille ferret facility and animal care personnel at Pueblo and F.E. Warren.

The National Zoo's Conservation and Research Center (CRC) provided logistical support, housing, food, and husbandry for captive polecats. The Pueblo Army Depot and CRC allowed us to convert buildings into polecat conditioning arenas. The Colorado Division of Wildlife and the Wyoming Game and Fish Department assisted in selecting study sites for polecat releases and granting necessary permits. Ranchers at Hasty, Veteran, and Shirley Basin graciously allowed us to work on their lands. J. Ma and Z. Zhao, Northeast Forestry University (Ministry of Forestry), Harbin, China, were instrumental in obtaining polecats from Inner Mongolia. The U.S. Army Corps of Engineers provided housing and office facilities at Hasty. L. Phillips of Brookfield Zoo and S.Monfort and J. Zoziarski of the National Zoo performed sterilization surgery on ferrets, and R. Opferman provided veterinary assistance on many occasions. Space does not permit individual acknowledgment of the many technicians and volunteers who worked on ferret releases, but their help is sincerely appreciated. Heather Branvold graciously agreed to provide the comparative drawings of the Siberian polecat and black-footed ferret.

TABLE OF CONTENTS

PAGE

CHAPTER 1. INTRODUCTION 1
LITERATURE CITED 6

CHAPTER 2. EFFECT OF CAPTIVITY ON BOLDNESS OF SIBERIAN POLECATS AND BLACK-FOOTED FERRETS 11
ABSTRACT 11
METHODS 15
Subjects 15
Testing procedure 17
Attributes measured 18
Analyses 19
RESULTS 22
Generation 22
Comparisons between black-footed ferrets and Siberian polecats 22
Assessment of risk 23
Intra-animal consistency in boldness 24
Learning by repetition 24
DISCUSSION 25
Generational changes 25
Assessment of risk 27
Intra-animal consistency in boldness 28
Learning by repetition 29
Boldness tradeoffs and natural selection 30
Conservation 33
REFERENCES 34

CHAPTER 3. MORTALITY OF SIBERIAN POLECATS AND BLACK-FOOTED FERRETS DURING EXPERIMENTAL RELEASES ON PRAIRIE DOG COLONIES 47
ABSTRACT 47
INTRODUCTION 48
METHODS 49
Study sites 49
Rearing 51
Release 52
Radio-telemetry 53
Classification of mortality 54
Modeling mortality rate–general methods 55
Surveys of predators and alternative prey 57

Effect of rearing and release methods 57
Predation and starvation 58
Body mass 58
Captive-born and wild-born polecats and ferrets 58
RESULTS 59
Surveys of predators and alternative prey 61
Effect of rearing and release methods 61
Predation and starvation 63
Body mass 64
Captive-born and wild-born polecats and ferrets 65
DISCUSSION 65
LITERATURE CITED 72

CHAPTER 4. TEMPORAL AVOIDANCE OF PREDATORS BY SIBERIAN POLECATS AND BLACK-FOOTED FERRETS 85
ABSTRACT 85
INTRODUCTION 86
METHODS 89
Study sites and subjects 89
Radiotelemetry 90
Animal activity 91
Monitoring activity using estimates of location 93
Monitoring activity using pulse interval 94
Diel periods and lunar measures 94
Use and availability 94
Rearing backgrounds and sexes of animals 98
Black-footed ferret and coyote activity patterns 99
Siberian polecat and red fox activity patterns 100
RESULTS 100
Data overview 100
Telemetry error 101
Independence of bouts 101
Species 102
Day and night 102
Moon 103
Black-footed ferret and coyote activity patterns 104
Siberian polecat and red fox activity patterns 104
DISCUSSION 104
Moonlight 104
Intraguild predation (IGP) and diel patterns of activity 105
Intraguild predation and black-footed ferret populations 109
Individual fitness, other considerations 111
Telemetry error 112

Management implications 113
LITERATURE CITED 114

CHAPTER 5. THE EFFECT OF REARING METHODS ON SURVIVAL OF REINTRODUCED BLACK-FOOTED FERRETS 135
ABSTRACT 135
METHODS 138
Rearing Strategies 138
Release 141
Monitoring 142
Statistical Procedures 143
RESULTS 146
Comparison of PENRES and CAGE Animals 146
Comparison of PENRES, PEN60 and PEN90 Animals 147
Comparison of Males and Females 147
DISCUSSION 148
MANAGEMENT IMPLICATIONS 152
LITERATURE CITED 153

CHAPTER 6. CONCLUDING REMARKS AND RECOMMENDATIONS .. 165
Predation Avoidance 165
Generalist and Specialist 167
Yersinia pestis as a Predator 171
Plague, Fluctuating Prey Populations, and r-K Selection 172
Predator Avoidance Behaviors 175
Generational Changes and Rearing Environments 178
LITERATURE CITED 180

CHAPTER 1

INTRODUCTION

The following studies of black-footed ferrets (Mustela nigripes) and Siberian polecats (M. eversmannii) were prompted primarily by the precarious status of black-footed ferrets, which had become extremely rare by the 1960s, and were reduced to a single known population in Wyoming by 1981 (Clark, 1989). The cause of the decline was attributed primarily to reduction in habitat due to losses of prairie dogs (Cynomys spp.) from agricultural conversion and direct poisoning campaigns. The ferrets' problems were exacerbated by introduced plague (Yersinia pestis) which reduced or elimated prairie dogs in wide areas (Barnes, 1993) and can cause direct mortality in ferrets (Williams et al., 1994, 1996), from canine distemper (Forrest et al., 1988;Williams et al.,1988), and by other interacting factors resulting from population isolation (Biggins and Schroeder, 1988). By 1985, the Wyoming population was threatened with extirpation due to concurrent outbreaks of plague and distemper, and was reduced to 10 individuals by the winter of 1985-86. Remaining animals were captured by 1987 to begin a captive breeding effort (Miller et al., 1996). At its onset, a primary goal of captive breeding was to provide ferrets for reintroduction (U. S. Fish and Wildlife Service, 1988). After a tenuous start, the expanding captive population produced sufficient numbers of black-footed ferrets to allow

reintroduction to begin in 1991. A portion of the data for this dissertation (Chaps. 3-5) was derived from ferret releases in 1991-1995.

Siberian polecats were used as investigational surrogates during the first efforts to breed black-footed ferrets in captivity in the 1970s (Carpenter, 1985), and again during the current effort. Use of polecats enhanced understanding of reproductive cycles and enabled development of manipulative techniques (Mead and Neirinckx, 1990; Mead et al., 1990; Williams et al., 1992). When reintroduction became a likely prospect, behavioral development and effects of rearing methods were studied in polecats (Miller et al., 1990a, b), followed by studies conducted in 1989-1996 (described herein) to examine behavioral changes in captivity, and to develop rearing and reintroduction strategies.

North American black-footed ferrets and Siberian polecats are musteline members of the family Mustelidae (Wilson and Reeder, 1993), but their taxonomic status at the generic level and below has been debated. Youngman (1982) combined the three polecats and ferrets (including the European polecat, M. putorius) into the subgenus Putorius, whereas Russian scientists (Ognev, 1931; Stroganov, 1962) tend to elevate Putorius to genus, reserving use of Mustela for weasels. Opinions vary on designating species, from suggestions of conspecificity for all ferrets and polecats (Heptner et al., 1967) or conspecificity of black-footed ferrets and Siberian polecats (Kurtén and Anderson, 1980) to separating M. amurensis from the remainder of the M. eversmannii group (Gao, 1987), but with most authors favoring three species within the subgenus (M. eversmannii, M. putorius, and M. nigripes). Fertile offspring result from "hybridization" of Siberian polecats with European polecats (Ternovskii, 1977) and with black-footed ferrets

(Davison et al., 1999). Varying numbers of subspecies have been described for M. eversmannii and M. putorius (Stroganov, 1962; Heptner et al., 1967), but Anderson et al. (1986) found no support for assigning subspecies within M. nigripes.

Although black-footed ferrets and Siberian polecats are similar in size (total length ≈ 50 cm), Siberian polecats are much more variable across their large range. Masses of female Siberian polecats vary from about 400 g for M. e. amurensis (= M. amurensis) to about 1100 g for M. e. larvatus in China (Gao, 1987). Males of polecats and ferrets vary similarly among subspecies, and are about 50% heavier than females. Black-footed ferrets could not be distinguished from Siberian polecats using cranial characteristics (Anderson et al., 1986), but Siberian polecats have longer guard hair giving a generally shaggier appearance, and throat and chest areas of the polecats are comparatively dark (Fig. 1.1).

The range of Siberian polecats extends from eastern Europe across Asia nearly to the Pacific Ocean (> 7500 km), and from about 30° N. latitude in China and Tibet to 60° N. in Siberian Russia. The historic range of black-footed ferrets was relatively narrow (east to west), but has a similar 30-50° extent in latitude, resulting in a total area about 80% smaller than the range for Siberian polecats. Both typically inhabit broad open steppes, but also occur in grassland islands within forested areas. The range of black-footed ferrets coincides with the collective ranges of three species of prairie dogs (Cynomys ludovicianus, C. leucurus, and C. gunnisoni), which serve as prey and provide high densities of burrows used by the ferrets. Although susliks (Spermophilus spp.) predominate in the diet of Siberian polecats over a large portion of their range (Brom, 1954; Chelnokov et al.,1979; Densiov, 1984; Serrebrennikov, 1929; Stroganov, 1962), the

polecats' distribution is not limited to the range of susliks, extending for example, over a large expanse of the Tibetan plateau in western China, where they locally may depend on alpine grassland colonies of pikas (Ochotona spp.), and zokors (Myospalax spp.) (Zheng et al., 1983). To the north, the range of Siberian polecats is limited by the taiga, which they do not inhabit except where agricultural conversion has taken place (Stroganov, 1962).

The opportunity to contrast the behaviors of polecats and ferrets under standardized laboratory conditions, and under similar ecological conditions in the wild, was intriguing from an evolutionary perspective, a recurrent theme of Chaps. 2-4. An improved understanding of the comparative behaviors of these animals also may help define the limits for using polecats as a model for black-footed ferrets. Finally, because of the fertility of polecat-ferret hybrids, the door is left ajar regarding hybridization as a management tool to extract the black-footed ferret from what may be an extreme case of depauperate genetic variation (O'Brien et al., 1989) left from population bottlenecks in the wild and inbreeding in captivity. Notwithstanding the debate over conspecificity and the characterization of black-footed ferrets and Siberian polecats as ecological equivalents (Hoffmann and Pattie, 1968), behavioral distinctiveness of Siberian polecats and black-footed ferrets should be an important topic in any such discussion .

Predation is a central focus of this treatise partly because predator avoidance often requires complex behaviors that could be vulnerable to alteration in captivity. Second, predation was the primary cause of loss of radio-tagged black-footed ferrets in the

Meeteetse, Wyoming population (Forrest et al., 1988), causing concern that even small changes in behavior mediated by captivity could be catastrophic for released animals.

Predation avoidance strategies in animals broadly include morphological and behavioral adaptations that reduce the risk of predation. Predator avoidance, as used herein, is a subset of predation avoidance strategies limited to behaviors of a prey organism that serve to reduce probability of contact with its predators, including canalized diel patterns of activity, choices in activity based on sensory risk assessment, and a prey's flight following detection by a predator.

Studies of predation on Mustela spp. are scarce (Korpimäki and Norrdahl, 1989a,b; Latham, 1952; Powell, 1973; Rosenzweig, 1966), relative to information available on other aspects of Mustela biology. King (1990), for example, devoted about 40 pages to how weasels (Mustela spp.) function as predators, compared to 5 pages discussing predation on weasels. King's (1990) citations reflect similar emphasis, with 15-fold more papers relating to hunting and killing by weasels as opposed to being killed by other predators. Evolutionary effects of predation, however, have been proposed, including explanations for the black-tipped tail of some weasels (also black-footed ferrets and Siberian polecats) (Powell, 1982), and white winter pelage (King, 1990). Predation has been suggested as an influential factor in population dynamics of Martes martes (Lindström et al., 1995) and Mustela erminea (Mulder, 1990).

Two events of the 1850's were highly influential in the discussions that follow. At the beginning of that decade, two well-known American naturalists, Audubon and Bachman (1851), described the black-footed ferret to the scientific world, and in the

decade's final year, Darwin (1859) initiated a paradigm that helped frame such taxonomic decisions in causal evolutionary theory. In each of the following chapters, the underlying theme of predation on Siberian polecats and black-footed ferrets is discussed in the context of comparative natural selection, and the implications for conservation of the ferret are emphasized.

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 Nat. Mem. 8:11-62.

Audubon, J. J., and J. Bachman. 1851. The viviparous quadrupeds of North America: Volume 2. V. G. Audubon, New York.

Barnes, A. M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pp. 28-37 in J. Oldemeyer, D. Biggins, B. Miller and R. Crete (eds.), Management of Prairie Dog Complexes for the Reintroduction of the Black-footed Ferret. U. S. Fish and Wildl. Serv. Biol. Rpt 93-13, Washington, D.C.

Biggins, D. E., and M. H. Schroeder. 1988. Historical and present status of the black-footed ferret. Pp. 93-97 in Proc. Eighth Great Plains Wildl. Damage Control Workshop, USDA Forest Service Gen. Tech. Rpt. RM-154, Fort Collins, Colorado.

Brom, I. P. 1954. Materials on the biology of the transbaikal polecat. Nauchno-Issledovatel'shogo Protivo-chumnogo Instituta Sibiri i Dalnego Vostoka 12:224-230.

Carpenter, J. W. 1985. Captive breeding and management of black-footed ferrets. Pp. 12.1-12.13 in S. H. Anderson and D. B. Inkley, eds., Proc. Black-footed Ferret Workshop, 18-19 Sep. 1984. Wyoming Game and Fish Dept., Cheyenne. 228 pp.

Chelnokov, V. N., Zuichenko, A., & Fedyashev, Yu. 1979. Fluctuations of the southern boundary of the range of the steppe polecat in western Turkmenia. Moskovskoe Obshchestvo Ispytatele i Prirody, Biulleten, 84:46-48.

Clark, T. W. 1989. Conservation biology of the black-footed ferret, Mustela nigripes. Wildlife Preservation Trust Special Scientific Report No. 3. Wildlife Preservation Trust International, Philadelphia, Pennsylvania.

Darwin, C. 1859. On the origin of species. Reprinted 1950. Watts and Co., London.

Davison, A., J. D. S. Birks, H. I. Griffiths, A. C. Kitchener, D. Biggins, and R. K. Butlin. 1999. Hybridization and the phylogenetic relationship between polecats and domestic ferrets in Britain. Biol. Cons. 87:155-161.

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 Hauk. 15:89-93.

Forest, S. C., D. E. Biggins, L. Richardson, T. W. Clark, T. M. Campbell, K. A. Fagerstone, and E. T. Thorne. 1988. Population attributes for the black-footed ferret (Mustela nigripes) at Meeteetse, Wyoming, 1981-1985. J. Mammal. 69: 261-273.

Gao, Y. (ed.). 1987. Fauna sinica, Mammalia, volume 8: Carnivora. Science Press, Bejing.

Heptner, V. G., N. P. Naumov, P. B. Yurgenson, A. A. Sludskii, A. F. Chirkova, and A. G. Bannikov. 1967. Mammals of the Soviet Union: Sea Cows and Carnivores (Volume 2). Vysshaya Shkola, Moscow.

Hoffmann, R. S. and D. L. Pattie. 1968. A guide to Montana mammals. University of Montana, Missoula. 133 pp.

King, C. 1990. The natural history of weasels and stoats. Cornell University Press. Ithaca, New York. 253 pp.

Korpimäki, 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.

_____, and _____. 1989b. Avian predation on mustelids in Europe 2: impact on small mustelid and microtine dynamics–a hypothesis. Oikos 55:273-276.

Kurtén, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York.

Latham, R. M. 1952. The fox as a factor in the control of weasel populations. J. Wildl. Manage. 16:516-517.

Lehner, P. N. 1998. Handbook of ethological methods, second edition. 672 pp. Cambridge University Press, UK.

Lindström, E. R., S. M. Brainerd, J. O. Helldin, and K. Overskaug. 1995. Pine marten–red fox interaction: a case of intraguild predation? Ann. Zool. Fennici 32:123-130.

Mead, R. A., and S. Neirinckx. 1990. Photomanipulation of sexual maturation and breeding cycle of the steppe polecat (Mustela eversmanni) and other techniques for more rapid propagation of the species. J. Exp. Zool. 255:232-238.

_____, _____, and N. M. Czekala. 1990. Reproductive cycle of the steppe polecat (Mustela eversmanni). J. Repro. and Fert. 88:353-360.

Miller, B., D. Biggins, C. Wemmer, R. Powell, L. Hanebury, D. Horn, and A. Vargas. 1990a. Development of survival skills in captive-raised Siberian polecats (Mustela eversmanni) I: locating prey. J. Ethology 8:89-94.

_____, _____, _____, _____, L. Calvo, L. Hanebury, and T. Wharton. 1990b. Development of survival skills in captive-raised Siberian polecats (Mustela eversmanni) II: predator avoidance. J. Ethology 8:95-104.

_____, R. P. Reading, and S. Forrest. 1996. Prairie night. Smithsonian Institution 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.

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. Pages 21-33 in Conservation biology and the black-footed ferret. Yale University Press, New Haven, CT.

Ognev, S. I. 1931. Mammals of eastern Europe and northern Asia, Carnivora, Fissipedia, Vol. II. Israel Program for Scientific Translations, Jerusalem.

Powell, R. A. 1973. A model for raptor predation on weasels. J. Mammal. 54:259-263.

_____. 1982. Evolution of black-tipped tails in weasels: predator confusion. Amer. Nat. 119:126-131.

Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. J. Mammal. 47:602-612.

Serrebrennikov, M. K. 1929. The steppe polecat (Putorius eversmanni) in the Wermut steppes of northern Kazakhstan. Zeithschrift für Säugetierkunde 4:205-212.

Stroganov, S. U. 1962. Carnivorous Mammals of Siberia. Translation: Israel Program for Scientific Translations, Jerusalem, 1969. U.S. Dept. Commerce, Clearinghouse for Federal Scientific and Technical Information, Springfield, Virginia 22151.

Ternovskii, D. V. 1977. Biology of the mustelids (Mustelidae). Nauka, Novosibirsk.

U.S. Fish and Wildlife Service. 1988. Black-footed ferret recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado. 154 pp.

Youngman, P. M. 1982. Distribution and systematics of the European mink, Mustela lutreola Linnaeus 1761. Acta Zool. Fennica 166, 1-48.

Williams, E. S., K. Mills, and A. Boerger-Fields. 1996. Plague in orally exposed black-footed ferret x Siberian polecat hybrids. Abstract In Forty-fifth Annual Conference of the Wildlife Disease Association, July 21-25, 1996, Fairbanks, Alaska.

_____, _____, D. R. Kwiatkowski, E. T. Thorne, and A Boerger-Fields. 1994. Plague in a black-footed ferret (Mustela nigripes). J. Wildl. Dis. 30:581-585.

_____, E. T. Thorne, M. J. G. Appel, and D. W. Belitsky. 1988. Canine distemper in black-footed ferrets (Mustela nigripes) from Wyoming. J. Wildl. Dis. 24:385-398.

_____, _____, D. R. Kwiatkowski, K. Lutz, and S. L. Anderson. 1992. Comparative vaginal cytology of the estrous cycle of black-footed ferrets, Siberian polecats, and domestic ferrets. J. Vet. Diagn. Invest. 4:38-44.

Wilson, D. E., and D. M. Reeder (eds). 1993. Mammal species of the world: a taxonomic and geographic reference, second edition. Smithsonian Press, Washington, D.C.

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(1):35-46.

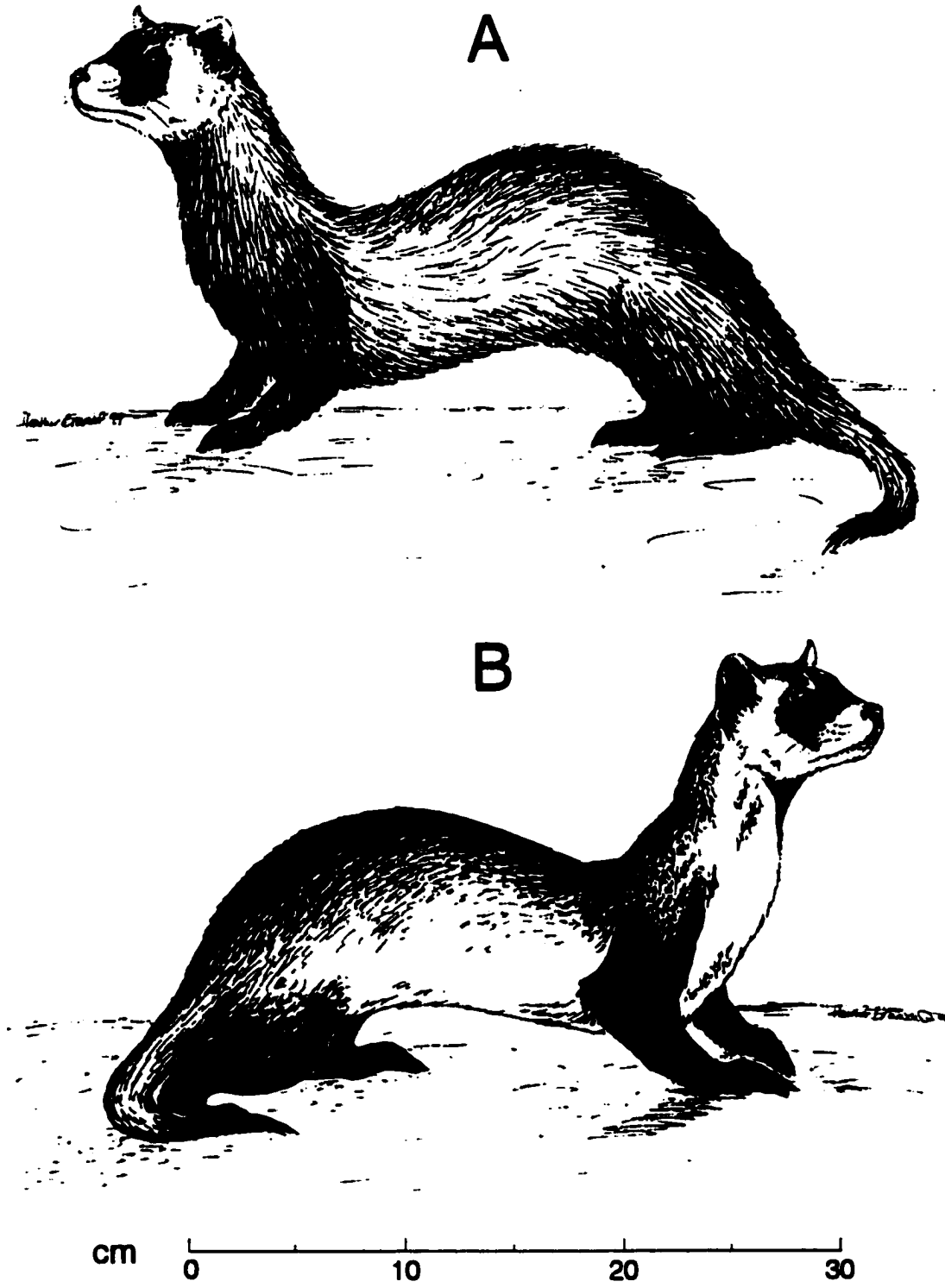

Figure 1.1. (A) Siberian polecat (Mustela eversmannii dauricus) and (B) black-footed ferret (M. nigripes).

CHAPTER 2

EFFECT OF CAPTIVITY ON BOLDNESS OF SIBERIAN POLECATS AND BLACK-FOOTED FERRETS[1]

ABSTRACT

Black-footed ferrets (Mustela nigripes) apparently persist only in captivity and in several small reintroduced populations. Concerns about the effect of captivity were prompted by high postrelease predation rates on ferrets. We used Siberian polecats (M. eversmannii), which are closely related to black-footed ferrets, to study changes in anti-predator behaviours during four generations of captivity, and behaviours of the two mustelids were compared. We investigated boldness, a fundamental psychological attribute of animals linked to ecological tradeoffs in foraging and predator avoidance, as individuals explored a novel arena and were subjected to simulated attack from a stuffed owl. For polecats (n=88), median durations to complete the entire trial (pre-attack + post-attack phases) decreased from the first generation (108·2 min) to the fourth (5·3 min) generation (P=0·012 overall), implying increased boldness. The post-attack flight to burrow was completed within 4 s by only 24 % of fourth generation polecats, compared to 77 % of first generation polecats (P=0·002 overall). Black-footed ferrets (n=12), in their third to

[1]Formatted for submission to *Animal Behaviour*

fifth generation of captivity, were significantly bolder than first generation polecats for most measures, but were similar to fourth generation polecats. Individual polecats tended to be consistent in boldness, as measured by the correlation between pre-attack and post-attack latencies to depart the burrow (R=0·536, P<0·001), and seemed to associate the attack with increased risk, indicated by a 12-fold increase in the post-attack latency of departure (P<0·001). Ferrets were inconsistent individually, and did not appear to recognize change in risk. Number of returns to the burrow during exploration was predictive of duration of the escape reaction for polecats (R=0·617, P<0·001), suggesting learning through repetition. Although captive propagation was essential for black-footed ferrets, recognition of progressive behavioural changes in captivity underscores the importance of conserving free-ranging populations of animals, and of expediting the reintroduction process.

Black-footed ferrets (Mustela nigripes) are North American mustelids that nearly became extinct in 1985 when epizootics of canine distemper and sylvatic plague swept through the last known colony near Meeteetse, Wyoming (Forrest et al. 1988; Williams et al. 1988). A captive breeding program was initiated using 10 survivors and their eight wild-born progeny, with the ultimate goal of reintroduction. Although captive production had a tentative beginning, by 1989 the prospect of ferret releases looked promising (Miller et al. 1996; Biggins et al. 1997). Initially, questions regarding effects of captivity on behaviours (and other attributes) of animals to be reintroduced could not be addressed

with the limited supply of highly valuable black-footed ferrets, but Siberian polecats (M. eversmannii) were used as investigational surrogates to study the maturational component of antipredator responses and other behaviours (Miller et al. 1990a, b). Siberian polecats are closely related to black-footed ferrets (Youngman 1982; O'Brien et al. 1989), and have been considered their Asian ecological equivalents (Hoffmann & Pattie 1968). Wild ancestry and breeding histories were unknown for those initial populations of Siberian polecats acquired mostly from European fur farms and zoos, motivating us to replicate the black-footed ferret's history of captivity with a small group of polecats (M. e. dauricus) captured in Inner Mongolia, China, and brought to the United States for captive breeding.

Domestication, intentional or inadvertent, is a result of genetic changes from modified selective pressure (Kohane & Parsons 1988) and continued maintenance of animals in artificial environments that modify opportunities for learning (Clark & Galef 1977). Producing truly wild animals in an artificial environment may be impossible (Spurway 1955; Vincent 1960). Antipredator behaviours can be lost quickly in captivity, even in wild-caught individuals (Ward et al. 1996). Post-release predation rates have been high on captive-born black-footed ferrets and Siberian polecats (Chaps. 3, 5). Nonetheless, several varieties of domestic animals, including forms of Mustela spp. (Moors & Lavers 1981; Smal 1991), have invaded or re-invaded natural habitats, exemplifying reversibility of domestication. Moreover, rearing ferrets and polecats in a quasi-natural environment increased post-release survival (Chap. 3, 5; Biggins et al. 1999). From these varying perspectives, the role of captive breeding in conservation has been debated (Varner & Monroe 1991; Lindberg 1994).

Boldness (the degree of hesitancy when confronted with danger) is a fundamental psychological characteristic of animals that has been connected with various life history tradeoffs concerning foraging, predation, and social interactions (Wilson et al. 1993; Budaev 1997). Within populations of captive animals, mean levels of boldness may be altered intentionally (Belyaev 1979; Hansen 1996) or unintentionally (Vincent 1960; Swain & Riddell 1989). Although the term "trait" may be inappropriate for describing the flexibility in expression of boldness (fearlessness) which seems to respond to a wide variety of environmental influences (Wilson et al. 1994), the ability to select artificially for or against boldness in captive populations of animals is consistent with requisite heritability of traits. Measures of boldness thus are repeatable within individuals of at least some species (Kagan 1991; Suomi 1991; Wilson et al. 1993), although the measures used as indicators of the trait incorporate additional sources of variation (e.g., transitory motivational states, degree of satiation, unmeasured and uncontrolled variation in the test environment). Historically, attention to individual variation was motivated mostly by its profound statistical effect on ability to detect differences in central tendencies among treatment groups. Because selection operates on variation at the individual level, studies of variation among individuals have intrinsic merit (Svendsen 1974; Armitage 1986; Coss & Biardi 1997; Hayes & Jenkins 1997). We predicted consistency in boldness of individual polecats during exploration of a novel environment and after attack by a mock predator.

Excessive boldness may increase the vulnerability of released black-footed ferrets to predation, whereas excessively shy ferrets may be poor hunters and killers. Both extremes may impede successful reintroduction of ferrets. Thus, the main objective of this

study was to examine changes in boldness of polecats (as investigative surrogates for ferrets) during four generations of captivity. We also examined changes in behaviours of individual polecats that may be attributed to learning. We predicted that polecats would be less bold after the attack due to perception of increased risk, and that learning by repeatedly retreating to a "burrow" would enhance the escape response to a mock predator (a stuffed owl on a pendulum). We compared ferrets and polecats using several boldness attributes to evaluate the suggestion of ecological equivalence of the two species.

METHODS

Subjects

Founder histories of our black-footed ferrets and Siberian polecats were similar. Both groups stemmed from six wild caught animals. For ferrets, our experimental group can be traced to three males and three females, but one male was heavily represented due to his early breeding success in the captive program. The captive population of polecats began with five females, but only one male. Distinct generational identity was maintained in polecats of this experiment by breeding females with males from the same generation. Inter-generational breeding of black-footed ferrets, however, was routine. Because males do not contribute to the rearing of ferret and polecat kits, most cultural influences are maternal; cultural and genetic definitions of generation thus differed in black-footed ferrets. The term generation here refers to the number of females in the direct maternal line from the first captive-born female to the subject (inclusive), ignoring the male genetic contribution.

The 12 black-footed ferrets used in this study, obtained in 1992, were surplus to the captive-breeding program for this endangered species. We transferred 5-month-old, cage-reared ferrets to an experimental facility at the Pueblo Army Depot, Pueblo County, Colorado, where their primary function was to produce kits for other experiments on rearing methods (Chap. 5). The 88 Siberian polecats used in this experiment were produced during 1992-1996, stemming from wild-caught ancestors captured in Inner Mongolia, China and transported to the United States in 1992. The 13 first-generation captive-born polecats were born at an interim holding facility and shipped to the Pueblo Army Depot when kits were 3 months old. Other polecats in the experiment (38 third generation and 37 fourth generation) were produced at the Pueblo Army Depot. Second generation polecats were not tested for this experiment.

We raised ferrets and polecats in cages constructed of wood and wire mesh, with floor area of 1·5 m^2 (Williams et al. 1991). Cages were supported aboveground on 1 m legs, and flexible plastic tubing (10 cm diameter) allowed access to a belowground nest box of 0·24 m^2 floor area (top of box was 10 cm subsurface). We fed ferrets and polecats commercial mink chow and cleaned their cages daily. Cages were housed in barns that were variously open to outdoor conditions (20-50 % exposed), with dirt floors, natural lighting and uncontrolled temperatures. Due to the semi-open barns, the environment presented a greater variety of natural stimuli than did standard indoor ferret production facilities. We often heard calls of predators such as great-horned owls (Bubo virginianus), barn owls (Tyto alba), and coyotes (Canis latrans) at night, sometimes at close range. We commonly observed small mammals (notably Peromyscus maniculatus and Neotoma sp.)

in the barns, and ferrets and polecats occasionally ate them. We also saw reptiles (Pituophis catenifer, Masticophis flagellum, Crotalus viridus, Sceloporus undulatus) and birds (Sturnella neglecta, Passer domesticus, Tyrannus tyrannus, Hirundo rustica, Columba livia, Tyto alba, Bubo virginianus) in the barns.

Testing procedure

We tested 6-month-old ferrets and polecats in two 3·38-m by 3.38-m arenas having retaining walls 1·14 m high (Fig. 2.1). Arenas were in buildings separated from the rearing barns. Before beginning a series of trials, non-test polecats or ferrets were kept in the test arena for at least 1 d to pre-condition the arena with scent. The nest box used as shelter during the trial (0·22 m^2 floor area) was left in the test subject's cage for familiarization for 24 h prior to the trial, and bedding from the subject's fixed nest box was added to the test box. We moved a subject from its cage to the arena in the test box 2 h prior to the trial, and placed the box in position within the false floor of the arena (Fig. 2.1). We placed food and water 3·4 m from the "burrow" opening in the test box. A small electric heater with continuous fan moderated the temperature and provided "white noise" in the building containing the arena. We conducted tests at night with a 3-watt light illuminating the arena to simulate full moon, preferred conditions for activity of polecats and ferrets (Chap. 4). We alternated males and females in successive trials within an arena in an attempt to maintain a consistent pattern of odors. We allocated sexes as equally as possible to the two test arenas. We monitored each trial for 8 h with a video camera mounted in the arena (Fig. 2.1), linked to a video cassette recorder in an adjacent building. An infrared light source augmented illumination from the 3-watt bulb. To begin a trial, we

manually removed the sliding door on top the nest box and immediately left the building. When the subject had moved within the arena sufficiently to intercept the beam to an infrared sensor (about 2.5 m from the opening to the nest box), a switch was closed, triggering the door of the owl's box to open (Fig. 2.1). Action of the falling door released a stuffed great-horned owl mounted on a pendulum, and counter-weights hastened its flight diagonally through the arena to the top of its semi-circular arc, where it came to rest in the opposite corner. We extracted data by reviewing the videotape and using event recording software (by DEB) to code changes in status of the subject with regard to its visibility in the burrow, and its movements away from and into the 0·25 m^2 cell surrounding the burrow (Fig. 2.1). Crossings of the cell's boundary were considered complete when all four feet had crossed the line. Because the owl was not within the camera's field of view in the upper parts of its flight, we recorded time of owl attack at the bottom of its arc.

Attributes measured

We used the total duration for a trial, measured from the animal's first appearance in the burrow until its post-attack redeparture from the burrow cell, as an overall index of boldness and used this measure for an omnibus test of generational effect. We interpreted decreased total time as increased boldness. The only measure included within total time that would be expected to increase with increasing boldness was duration of post-attack flight to the burrow, which characteristically was completed so quickly as to constitute a negligible portion of the total time.

We used seven additional measures for more detailed descriptions and comparisons. Total time of trial was subdivided into four mutually exclusive latencies separating the following: first appearance at burrow, first departure from burrow cell, owl attack, first post-attack return to burrow (mentioned above), and first post-attack departure from burrow cell. In the pre-attack period, two states, time within burrow cell and away from burrow cell, were cumulatively quantified, which summed to total pre-attack time minus time spent out-of-sight in burrow (the latter state was not analyzed). Frequency of an event, return to the burrow cell, also was tallied during the pre-attack period.

Analyses

An initial attempt at analyzing the effect of generation using multivariate general linear models resulted in residual variation that was heteroscedastic and non-normal. Distributions were skewed, outliers were common, and residuals could not be stabilized with traditional transformations that retained the continuous form of data. Thus, we adopted distribution-free statistical methods employing rank-transformation for further assessments. For comparison of generations and species, we used Kruskal-Wallace and Mann-Whitney tests; statistics presented are the Chi-square approximations (H), and associated P values. We used the exact Chi-square procedure of Berry and Mielke (1985) for contingency table analyses.

The omnibus test of generational effect involved a Kruskal-Wallace analysis of variance performed on total time of trial. This conservative approach treated generation as a categorical variable, ignoring the pattern of change (slope) through generations. We

judged the result as significant if the probability of committing a Type I error was $\leq 0{\cdot}05$. We also used total time of trial to compare the black-footed ferret with each of the generations of Siberian polecats; the three pairwise contrasts were evaluated with a statistically conservative Bonferroni-adjusted $\propto$ level ($\propto = 0{\cdot}05/3 = 0{\cdot}017$).

It is useful to dissect the total time of trials into separate components because the details may disclose behaviours with different underlying causes. The resulting multiple comparisons of non-independent measures, however, complicate statistical inference. In this situation, Bonferroni adjustment of the rejection level is overly conservative (Kleinbaum et al. 1988), and was not used. We present the results of non-parametric comparisons in tabular form, but suggest caution in their interpretation.

We used relationships between different measures taken on the same animal to evaluate (1) the animals' assessment of change in risk associated with the owl attack, (2) inter-animal differences in boldness, and (3) the potential influence of pre-attack learning on post-attack behaviour. We used parametric least squares analyses (multivariate general linear models and paired t-tests) to compare multiple measurements made on individuals. For these cases, the assumptions of homoscedasticity normality, and linearity appeared reasonable when all variables (predictors and response) were log-transformed. Rationale and procedures are as follows:

(1) If ferrets and polecats associate the owl attack with increased risk, we expected an increased latency to depart the burrow cell post-attack compared to latency of initial departure. We used paired t-tests to compare the two latencies.

(2) If the boldness is a behavioural axis with attendant intra-animal consistency, we expected an animal's post-attack latency of departure from the burrow cell, although increased by higher perceived risk, to be positively correlated to its initial latency of departure. We used a multivariate linear model, with log-transformed latencies, to examine the relationship. The model controlled for generation as a continuous variable while testing the correlation between the two measures. The procedure accounted for potential "latent grouping" influences on Pearson product-moment correlations (Coss & Biardi 1997) without the loss of power accompanying a separate analysis of each generation.

(3) As an animal gains familiarity with the novel arena during exploration, its efficiency of flight to the burrow at the time of the owl attack may increase. The number of returns to the burrow during exploration seem particularly relevant as practice for escape flight. A significant correlation between returns and escape efficiency, however, could be interpreted as intra-animal consistency in boldness, as described above for the comparison between pre- and post-attack departure latencies. We used a multivariate model, again using generation as a control variable (continuous), to simultaneously assess the contributions of (a) a measure made before an animal had much opportunity to learn (initial latency to depart) and (b) a behaviour that allows learning (returns to the burrow) to account for variance in escape movement. Thus, variable (a) mostly reflects the consistency in boldness and variable (b) reflects consistency in boldness plus escape practice. Log transformation precluded using animals that made no returns, reducing the polecat subset to 61 animals.

RESULTS

Generation

Overall, polecats spent significantly less total time completing trials as generation in captivity increased (respective medians for generations 1, 3 &4 = 108·2, 95·2, 5·3 min.; H_2=8·867, P=0·012). In the pre-attack period, latency of initial departure from the burrow cell appeared to decrease (Table 2.1) through four generations of captive Siberian polecats (Fig. 2.2A), as did cumulative time within the burrow cell (Fig. 2.3A), cumulative time away from the cell (Fig. 2.3B), and number of returns to the cell (Fig. 2.4). Duration of the post-attack flight to the burrow tended to increase with increasing generation (Table 2.1)(Fig. 2.5A), and the latency to first post-attack departure from the burrow cell decreased with increasing generation (Fig. 2.5B). Subjects appeared to initiate their response as the door to the owl box opened (Fig. 2.1), but the box was not in the video camera's field of view. Elapsed time from the instant the solenoid switch released the door until the owl reached the bottom of its "flight" arc was 0·9 s, a constant which should be added to our measure (Fig. 2.5A) to assess total duration of the response. The most rapid response to the owl attack (1·8 s, including the initial 0.9 s) was made by a first generation polecat, and proportions of polecats completing their flight to the burrow within the moderate limit of 4 s decreased significantly (X^2_2=12·515, P=0·002) through generations 1, 3 and 4 (respectively, 77 %, 53 %, 24 %).

Comparisons between black-footed ferrets and Siberian polecats

The total time in trial for black-footed ferrets (median=9·5 min.) was significantly less than total time in trial for first generation Siberian polecats (median=108·2 min.,

H_2=5·728, P=0·017), but did not differ from total time for later generations of polecats (gen. 3 median=95·2 min., H_2=0·999, P=0·318; gen. 4 median=5·3 min., H_2=0·865, P=0·352). Compared to first generation polecats, ferrets tended to be bolder, having shorter latencies to depart the burrow cell and trip the owl, shorter cumulative times within and away from the cell, fewer returns to the cell, and longer post-attack flights to the burrow (Figs. 2.2-2.5). Fourth generation captive polecats (similar to the mean generation for black-footed ferrets tested), were similar to ferrets for most component measures (Table 2.1, Figs. 2.2-2.5).

Assessment of risk

Siberian polecats seemed to associate the simulated owl attack with increased hazard of aboveground activity. Their mean latencies to depart the burrow cell were longer for the post-attack period (Fig. 2.5B) than for the pre-attack period (Fig. 2.2A) by an average factor of 12·4 (paired t_{86}=10·990, P<0·001). Surprisingly, these latencies did not differ for black-footed ferrets (paired t_{11}=0·897, P=0·389). Although only 12 ferrets were tested, that sample size should have been adequate to detect a major response to our attempt to alter the perceived risk. For example, the most extreme subset of 12 polecats that could be drawn from our overall sample, the 12 fourth generation polecats with the smallest increases in post-owl latency to depart the burrow cell (3 of them exhibited decreases), showed a marginally significant increase in latency of post-attack departure (t_{11}=2·128, P=0·057).

Intra-animal consistency in boldness

Individual polecats tended to behave consistently within trials when comparing departures under two levels of risk. A positive within-animal correlation between pre- and post-attack latencies to depart the burrow cell was significant for Siberian polecats (R=0·536, partial $F_{1,84}$=24·384, P<0·001), but not for black-footed ferrets (R=0·019, $F_{1,10}$=0·004, P=0·953).

Learning by repetition

The experience gained in making repeated returns to the burrow during the process of exploration appeared to contribute to an efficient escape response for polecats. Using multiple regression (with generation as a control variable) on the subset of polecat data containing polecats that returned to the burrow at least once during the pre-attack period, number of returns was significantly predictive of escape time (partial $F_{1,57}$=21·846, P<0·001), in contrast to the lack of effect of latency of initial departure (partial $F_{1,57}$=0·104, P=0·749). Results were similar using a separate regression model for each predictor; number of returns was a better predictor of escape time (R=0·617, partial $F_{1,58}$=26·307, P<0·001) than was latency of initial departure (R=0·380, partial $F_{1,58}$=3·056, P=0·086). The marginal significance of the latter relationship suggested effect of intra-animal consistency in boldness, but flight-to-burrow seemed less influenced by boldness than by practice or learned cues relating to spatial orientation.

After deleting two animals with no returns from the already small black-footed ferret sample, the 3-parameter regression model with returns and initial departure latency

as predictors of post-owl departure latency was not significant overall ($F_{2,7}$=0·815, P=0·480).

DISCUSSION

Generational changes

The progressive change in behaviours of our polecats suggested intergenerational genetic or cultural transmission (whereas a more sudden change between any of the consecutive generations might have implicated an abrupt change in environment). Four generations seems to be a short span for detectable genetic change in a population of vertebrates. However, high environmental stress of captivity has led to rapid evolution (Kohane & Parsons 1988; Price 1999) in captive steelhead trout in no more than two generations (Reisenbichler & McIntyre 1976), and in captive mink (Mustela vison) in one generation (Hansen 1996).

Our data, nevertheless, do not provide evidence that behavioural differences between generations of polecats had a genetic basis. Cultural exchange from dam to offspring is a possible cause of generational change that could operate without any change in gene frequencies. Although recognition of predator stimuli appears to be innate in many species (Hirsch & Bolles 1980; Giles & Huntingford 1984; Curio 1993; Coss & Biardi 1997), several types of learning may influence predator recognition and antipredator responses (Tulley & Huntingford 1987; Magurran 1990; McLean & Rhodes 1991; Krause 1993; Mathis et al. 1996). Learning by observation, for example, decreased lingcod (Ophiodon elongatus) predation on Coho salmon that had been exposed visually to such predation (Olla & Davis 1989), and reduced sculpin (Cottus asper) predation on similarly

exposed steelhead trout (Berejikian 1994). Polecat and ferret dams may have had the opportunity to transmit culturally to their kits recognition of owls and other predators as hazardous, but lack of natural burrows may have impeded development of efficient reactions. The calling of great horned owls was audible frequently from the open barns that housed ferrets and polecats, and owls that hunted in the vicinity of (and even entered) the barns occasionally could have been seen by the caged animals. Experiences of individual young polecats and ferrets and their dams doubtless varied in this regard, and may have provided inadequate opportunity for persistent cultural transmission of fear reactions over multiple generations.

Furthermore, genetic and cultural influences interact, especially during early development. Evolutionary ramifications of such interactions were postulated early (Morgan 1896) and continue to be debated (Avital & Jablonka 1994). Culturally transmitted behaviours may modify the phenotypes on which natural selection or artificial selection continue to act (sensu Wcislo 1989).

Captivity may have caused changes in ferrets comparable to those noted for polecats. For most attributes measured, our black-footed ferrets (generations 3-5) were more similar to the fourth generation Siberian polecats than to the first generation polecats. We did not, however, attempt to document progressive changes between generations of black-footed ferrets. Our ability to reduce post-release mortality of black-footed ferrets by changing the rearing environment for kits (Chap. 5) implies that at least part of the effect of captivity was not due to genetic change in the population.

Assessment of risk

Novelty provided the widely used initial stressor (Suomi 1987) of our experiment, but we attempted to increase stress by the simulated owl attack. The sounds and sight of the suddenly opening door to the box with the owl seemed to be an adequate stimulus to initiate flight. In the case of burrow-dwelling species, this reaction to sudden presentation of stimuli (releasers) appears to be adaptive even in the absence of enemy recognition. Risk assessment can be conducted by a ferret or polecat more safely from the burrow. The stoop of the owl in our trials may have reinforced the perceived appropriateness of the initial reaction, increased flight speed, and delayed re-departure latency, but the degree of enemy recognition is unclear (salience of such dummies was reviewed by Curio 1993). Regardless of how Siberian polecats interpreted the collective stimuli of the attack, they responded by a greatly increased post-attack latency to depart the burrow, observable in all generations. Risk assessment thus seems to be part of the polecat repertoire of predator avoidance behaviours, in keeping with tactics of many other animals (summaries by Sih 1987; Lima and Dill 1990).

The lack of an altered post-attack response in black-footed ferrets was surprising, and could be interpreted as a failure for ferrets to recognize the change in risk. Perhaps the owl (or the sound of the box opening) was a less relevant stimulus to ferrets than to polecats, or the suitability of the artificial burrow as a refuge may have been perceived differently by ferrets than by polecats. The small sample size of ferrets (n=12) may have hindered our ability to detect small changes, but we should not have failed to detect a change as dramatic as that of the polecats. There appeared to be recognition of increased

risk after the owl attack in even the least responsive 12 animals that could be drawn from our fourth generation polecat sample. Black-footed ferrets thus seem comparatively less inclined than Siberian polecats to engage in this type of risk assessment. Failure to detect risk assessment under the conditions of our experiment, however, does not mean the tactic is lacking.

Intra-animal consistency in boldness

Consistency within individuals and variation among them are necessary for natural or artificial selection to operate. We regard the correlation of pre-attack and post-attack burrow departures for individual Siberian polecats as preliminary evidence for individuality in boldness, although our data are insufficient to demonstrate a genetic basis for that individuality. The failure to detect similar consistency in black-footed ferrets was surprising, and deserves further investigation with larger sample sizes. Individuality in boldness has been demonstrated for a wide variety of species (Fox 1972; Svendsen 1974; Armitage 1986; Suomi 1991; Wilson et al. 1993; Coss & Biardi 1997; Kagan 1991), and its mean level has been successfully manipulated via artificial selection in captive populations of carnivores (Belyaev 1979; Hansen 1996).

Our subjects' caution in initial exploration of the novel arena may have been due to simple neophobia, with presumed anti-predation benefits. Residual scent from previous occupants, however, may have made subjects apprehensive about intraspecific encounters (Hendrie et al. 1996). If aggression toward conspecifics and fearlessness toward predators are positively correlated attributes associated with a general boldness trait in polecats, the ability to identify the motive is not critical to our conclusions regarding boldness. In

stickleback fish (Gasterosteus aculeatus), the most socially aggressive individuals are the most fearless toward predators (Huntingford 1976; Tulley and Huntingford 1988), and in wolves (Canis lupus), socially dominant pups are bolder in other contexts (MacDonald 1983), including the killing of prey (Fox 1972). Although the degree of boldness may be consistent within individuals over a wide range of circumstances for many species, expression of the trait may be context-specific in other cases (Coleman and Wilson 1998; Suomi 1987).

Learning by repetition

The significant inverse correlation between number of returns to the burrow cell and duration of post-attack flight to the burrow suggests learning increased the efficiency of the escape reaction. Alternatively, shy animals simply may be both more responsive to the owl and more prone to making "false starts" when departing the burrow. When modeled jointly, the number of returns (which encompassed both learning opportunity and individual boldness) accounted for much more of the variation in escape time than did initial latency to depart (an indicator primarily of boldness). Contingency-specific practice thus is implicated as a part of efficient predator avoidance in polecats. Because polecats hand-reared by a human surrogate exhibited escape responses to the owl attack that were qualitatively similar to responses observed in this experiment (Biggins, unpublished data), burrow-directed flight is likely an innate species specific defense response (Bolles 1970). Learning by practice, however, is a potentially important modifier of the efficiency of that response. In stickleback fry, practice gained during pursuits by the male guardian may promote increased predator avoidance scores during subsequent tests (Tulley &

Huntingford 1987), similar to increased escape efficiency of guppies (Poecilia reticulata) previously chased by adult conspecifics (Goodey & Liley 1986). We have observed captive and wild black-footed ferret kits repeatedly dashing to burrows during interactions with littermates. In our arena experiment, practice may have helped animals gain familiarity with characteristics of the substrate (traction) and develop burrow entry tactics. Repetitive practice also may have enhanced memorization of the location of the burrow relative to other features of the arena so the response could be appropriately directed.

Boldness tradeoffs and natural selection

In many species the degree of boldness varies between individuals, and predispositions are heritable but modifiable by environment and age (Wilson et al. 1994). Costs are exemplified by the pervasive starvation/predation tradeoff (Lima and Dill 1990). If boldness is a general trait, excessively bold individuals may have high risk of predation (only top predators are exempt) while excessively shy individuals risk starvation and further reduction in fitness stemming from their subordinate social status. The optimal level of boldness likely varies with changing conditions of population density and environment, providing a mechanism for maintenance of polyphenism (West-Eberhard 1989; Smith & Skúli 1996) or phenotypic plasiticty (Scheiner 1993) within populations. For example, laboratory tested juvenile coho salmon (Oncorhynchus kisutch) from a stream where predatory trout (Oncorhynchus mykis and O. clarki) made up > 50 % of the the salmonid population were less intraspecifically aggressive (interpreted as more shy) than were coho salmon from a stream where trout were < 2 % of the number of the

salmonids (Rosenau & McPhail 1987), and individuals of the former strain were socially dominant when the two forms were held as mixed pairs.

Over long time spans, spatial and temporal variation in the environment, coupled with the advantages and disadvantages of boldness, likely present natural selection with a moving target regarding optimal expression of the trait for black-footed ferrets, and more dramatically for Siberian polecats. With shifting densities of prey and other predators, both the need for aboveground travel and the hazards of this activity may change, resulting in altered costs and benefits to boldness for ferrets and polecats. Compared to black-footed ferrets, Siberian polecats have high phenotypic variability (17 described subspecies) and greater heterozygosity (Villablanca 1996). Across their large range, polecats occupy a greater variety of habitats and prey upon a wider diversity of species than do ferrets. Because of periodically devastating epizootics of plague (Yersinia pestis) in its primary prey (Chelnokov et al. 1977), the polecats' environment also varies temporally, which may cause them to switch to alternate prey and concomitantly alter other behaviours (Chaps. 3, 4). Is flexibility best accommodated by genotypic variability, or by expanded phenotypic plasticity as a heritable trait? Phenotypic plasticity allows rapid response to environmental change, but its costs relate to arguments concerning costs and benefits of specialization and generalization (Wilson et al. 1994, Wilson & Yoshimura 1994) applying the adage that "a jack of all trades is master of none." On the other hand, the cost of producing variable phenotypes is investment in a portion of offspring that are suboptimally adapted for existing conditions (Lively 1989; Adler & Harvell 1990). Siberian polecats have larger litters than do black-footed ferrets (Forrest et al. 1985), an advantage in a "shotgun"

strategy of polymorphism (more dramatically exemplified by the coho salmon discussed above, with hundreds of offspring per female), but also is consistent with an ability to respond quickly in population growth when the varying environment is most favorable. Because plague has been introduced into North American prairie dogs, ferret prey in many areas now exhibit temporal oscillations in population that resemble those of Asian polecat habitat. Ferrets do not switch prey, and may lack the genetic variability needed to cope with increased environmental stochasticity over the short or long term.

Some anti-predation behaviours may be fixed, such as the species specific defense response of flight to a burrow, and others may involve conditional responses such as risk assessment and contingent behavioural adjustment (Sih 1987; Lima & Dill 1990). An example of comparative behavioural flexibility that seems analogous to our ferret and polecat comparisons comes from mayfies (Nesameletus ornatus) in New Zealand streams (McIntosh & Townsend 1994) with and without introduced brown trout (Salmo trutta). Mayfly populations from streams with trout were nocturnally active whether predators were present or absent. Mayflies from streams with native fish predators or fishless streams, however, did not exhibit a diel pattern of activity, but changed their activity when the native predator was present. The canalized behavioural pattern of mayflies in trout streams evolved during the 130 years of predatory pressure from trout, perhaps due to high cost of risk assessment or relatively low benefit of varying the response (McIntosh & Townsend 1994). Perhaps a similar explanation holds for black-footed ferrets, which showed no evidence of altering their behaviours when the level of risk changed in our laboratory tests, and exhibited a relatively inflexible diel pattern of activity that seemed

related to predator avoidance (Chap. 4). In contrast, our Siberian polecats (like the mayflies from the natural stream community) reduced activity under elevated risk in the laboratory, and data from numerous field studies of polecats have detected a wide variety of diel patterns that may accommodate variations in risk of predation and hunting tactics (reviewed in Chap. 4).

Conservation

Captive breeding is an essential tool for conservation of some species. Without captive breeding, black-footed ferrets likely would be extinct. Nevertheless, captive breeding has drawbacks. Although domestication has produced strains of fishes, for example, that reproduce better and grow faster in captivity (Vincent 1960; Reisenbichler & McIntyre 1977), the domestic strains often have traits that reduce fitness in wild environments (Mason et al. 1967; Swain & Riddell 1989; Johnsson & Abrahams 1991). Even though a program with the objective of reestablishing natural populations should attempt to avoid artificial selection, maintaining even quasi-wild phenotypes through many generations will be challenging at best. Even if generational changes such as those noted here for polecats are not heritable, the altered behaviours are likely to impede successful reintroduction (May 1991; Snyder et al. 1996). A captive environment with salient stimuli (e.g., soil for digging, burrows as refuges, sufficient space to engage in natural play behaviour) may aid the ontogeny and retention of critical behaviours (Curio 1993; Shepherdson 1994; Vargas 1994; Carlstead 1996; Shepherdson et al. 1998), but compromises are unavoidable. Recognition that some changes may be inevitable, progressive, and difficult to reverse underscores the importance of conserving species and

intact ecosystems in their wild states, and of expediting reestablishment of naturally self-sustaining populations if captive breeding has become necessary.

REFERENCES

Adler, F. R., & Harvell, C. D. 1990. Inducible defenses, phenotypic variability, and biotic environments. Trends in Ecol. and Evol., 5, 407-410.

Armitage, K. B. 1986. Individuality, social behavior, and reproductive success in yellow-bellied marmots. Ecology, 67, 1186-1193.

Avital, E., & Jablonka, E. 1994. Social learning and the evolution of behaviour. Anim. Behav., 48, 1195-1199.

Belyaev, D. K. 1979. Destabilizing selection as a factor in domestication. J. Heredity 70, 301-308.

Berejikian, B. A. 1994. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (Oncorhynchus mykiss) to avoid a benthic predator. Can. J. Fish. Aquat. Sci., 52, 2476-2482.

Berry, K. J., & Mielke, P. W. Jr. 1985. Subroutines for computing exact Chi-square and Fisher's exact probability tests. Ed. and Psych. Meas., 45, 153-159.

Biggins, D. E., Miller, B. J., Clark, T. W., & Reading, R. P. 1997. Management of an endangered species: the black-footed ferret. In: Principles of Conservation Biology Second Edition (Ed. by Meffe, G. K., & C. R. Carroll), pp. 420-426. Sinauer Assoc., Sunderland, Mass.

Biggins, D. E., Vargas, A., Godbey, J. L., & Anderson, S. H. 1999. Influence of prerelease experience on reintroduced black-footed ferrets (Mustela nigripes). Biol. Cons., 89, 121-129.

Bolles, R. C. 1970. Species-specific defense reactions and avoidance learning. Psych. Rev., 77, 32-48.

Budaev, S. V. 1997. Alternative styles in the European wrasse, Symphodus ocellatus: boldness-related schooling tendency. Env. Biol. Fishes, 49, 72-78.

Carlstead, K. 1996. Effects of captivity on the behavior of wild mammals. In: Wild Mammals in Captivity: Principles and Techniques (Ed. by D. G. Kleiman, M. E. Allen, K. V. Thompson, & S. Lumpkin), pp. 317-333. Chicago Univ. Press, Ill.

Chelnokov, V. N., Zuichenko, A., & Fedyashev, Yu. 1977. Fluctuations of the southern boundary of the range of the steppe polecat in western Turkmenia. Moskovskoe Obshchestvo Ispytatele i Prirody, Biulleten, 84, 46-48.

Clark, M. M., & Galef, B. G. 1977. The role of the physical rearing environment in the domestication of the Mongolian gerbil (Meriones unguiculatus). Anim. Behav., 25, 298-316.

Coleman, K., & D. S. Wilson. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. Anim. Behav., 56, 927-936.

Coss, R. G., & Biardi, J. E. 1997. Individual variation in the antisnake behavior of California ground squirrels (Spermophilus beecheyi). J. Mammal., 73, 294-310.

Curio, E. 1993. Proximate and developmental aspects of antipredator behavior. In: Advances in the Study of Behavior, Vol. 22 (Ed. by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, & M. Milinski), pp.135-238. Academic Press, New York.

Forrest, S. C., Biggins, D. E., Richardson, L., Clark, T. W., Campbell, T. M. III, Fagerstone, K. A., & Thorne, E. T. 1988. Population attributes for the black-footed ferret (Mustela nigripes) at Meeteetse, Wyoming, 1981-1985. J. Mammal., 69, 261-273.

_____, T. W. Clark, L. Richardson, D. Biggins, K. Fagerstone, and T. M. Campbell III. 1985. Life history characteristics of the genus Mustela, with special reference to the black-footed ferret, Mustela nigripes. Pp. 23.1-11.14 in S. W. Anderson and D. B. Inkley (eds.), Black-footed Ferret Workshop Proceedings, Wyoming Game and Fish Department, Cheyenne.

Fox, M. W. 1972. Socio-ecological implications of individual differences in wolf litters: a developmental and evolutionary perspective. Behaviour, 41, 298-313.

Giles, N., & Huntingford, F. A. 1984. Predation risk and inter-population variation in anti-predator behaviour in the three-spined stickelback, Gasterosteus aculeatus L. Anim. Behav., 32, 264-275.

Goodey, W., & Liley, N. R. 1986. The influence of early experience on escape behaviour in the guppy (Poecilia reticulata). Can. J. Zool., 64, 885-888.

Hansen, S. W. 1996. Selection for behavioural traits in farm mink. Applied Animal Behaviour Science, 49, 137-148.

Hayes, J. P., & Jenkins, S. H. 1997. Individual variation in mammals. J. Mammal., 78, 274-293.

Hendrie, C. A., Weiss, S. M., & Eilam, D. 1996. Exploration and predation models of anxiety: Evidence from laboratory and wild species. Pharm. Biochem. and Behav., 54, 13-20.

Hirsch, S. M., & Bolles, R. C. 1980. On the ability of prey to recognize predators. Z. Tierpsychol., 54, 71-84.

Hoffmann, R. S.,& Pattie, D. L. 1968. A guide to Montana mammals. U. Montana, Missoula.

Huntingford, F. A.1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, Gasterosteus aculeatus. Anim. Behav., 24, 245-260.

Johnsson, J. I., & Abrahams, M. V. 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (Oncorhynchus mykiss): an experimental study. Can. J. Fish. Aquat. Sci., 48, 243-247.

Kagan, J. 1991. Continuity and discontinuity in development. In: Plasticity of Development (Ed. by S. E. Brauth, W. S. Hall, & R. J. Dooling), pp. 11-27. MIT Press, Cambridge, Mass.

Kleinbaum, D. G., L. L. Kupper, & K. E. Muller. Applied Regression Analysis and Other Multivariable Methods. PWS-KENT Publ. Co., Boston.

Kohane, M. J., & Parsons, P. A. 1988. Domestication, evolutionary change under stress. Evolutionary Biology, 23, 31-48.

Krause, J. 1993. Transmission of fright reaction between different species of fish. Behaviour, 127, 37-48.

Lima, S. L., & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool., 68, 619-640.

Lindburg, D. W. 1994. Better dead than captive bred? Zoo Biol., 13, 1-2.

Lively, C. M. 1989. Canalization versus developmental conversion in a spatially variable environment. Amer. Nat., 128, 561-572.

MacDonald, K. 1983. Stability of individual differences in behavior in a litter of wolf cubs (Canis lupus). J. Comp. Psych., 97, 99-106.

Magurran, A. E. 1990. The inheritance and development of minnow anti-predator behaviour. Anim. Behav. 39, 834-842.

Mason, J. W., Brynildson, O. M., Degurse, P. E. 1967. Comparative survival of wild and domestic strains of brook trout in streams. Trans. Amer. Fish. Soc., 96, 313-319.

Mathis, A., Chivers, D. P., & Smith, J. F. 1996. Cultural transmission of predator recognition in fishes: intraspecific and interspecific learning. Anim. Behav., 51, 185-201.

May, R. 1991. The role of ecological theory in planning the re-introduction of endangered species. Symp. Zool. Soc. London, 62, 145-163.

McIntosh, A. R., & Townsend, C. R. 1994. Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. Ecology, 75, 2078-2090.

McLean, I. G., & Rhodes, G. 1991. Enemy recognition and response in birds. Curr. Ornith., 8, 173-211.

Miller, B., Biggins, D., Wemmer, C., Powell, R., Calvo, L., Hanebury, L., & Wharton, T. 1990a. Development of survival skills in captive-raised Siberian polecats (Mustela eversmanni) II: predator avoidance. J. Ethol.8, 95-104.

Miller, B., Biggins, D., Wemmer, C., Powell, R., Hanebury, L., Horn, D., & Vargas, A. 1990b. Development of survival skills in captive-raised Siberian polecats (Mustela eversmanni) I: locating prey. J. Ethol., 8, 89-94.

Miller, B., Reading, R., & Forrest, S. 1996. Prairie Night--Black-footed Ferrets and the Recovery of Endangered Species. Smithsonian Press, Wash., D.C.

Moors, P. J., & Lavers, R. B. 1981. Movements and home range of ferrets (Mustela furo) at Pukepuke Lagoon, New Zealand. New Zealand J. Zool., 8, 413-422.

Morgan, C. L. 1896. On modification and variation. Science, 4, 733-740.

O'Brien, S. J., Martenson, J. S., Eichelberger, M. A., Thorne, E. T., & Wright, F. 1989. Biochemical genetic variation and molecular systematics of the black-footed ferret, Mustela nigripes. In: Conservation Biology and the Black-footed Ferret (Ed. by E. T. Thorne, M. A. Bogan, & S. H. Anderson), pp. 21-33. Yale Univ. Press, New Haven, Conn.

Olla, B. L., & Davis, M. W. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (Oncorhynchus kisutch) juveniles. Aquaculture, 76, 209-214.

Price, E. O. 1999. Behavioral development in animals undergoing domestication. Applied Anim. Behav. Sci., 65, 245-271.

Reisenbichler, R. R., & McIntyre, J. D. 1976. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, Salmo gairdneri. J. Fish. Res. Board Can., 34, 123-128.

Rosenau, M. L., & McPhail, J. D. 1987. Inherited differences in agonistic behavior between two populations of coho salmon. Tran. Amer. Fish. Soc., 116, 646-654.

Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. Annu. Rev. Ecol. Syst., 24, 35-68.

Shepherdson, D. 1994. The role of environmental enrichment in the captive breeding and reintroduction of endangered species. In: Creative Conservation: Interactive Management of Wild and Captive Animals (Ed. by P. J. S. Olney, G. M. Mace, & A. T. C. Feistner), pp. 167-177. Chapman & Hall, London.

Shepherdson, D. J., Mellen, J. D., & Hutchins, M. 1998. Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press, Wash. D. C.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In: Predation: Direct and Indirect Impacts on Aquatic Communities (Ed. by W. C. Kerfoot & A. Sih), pp. 203-224. Univ. Press of New England, Hanover, New Hampshire.

Smal, C. M. 1991. Population studies on feral American mink Mustela vison in Ireland. J. Zool., London, 224, 233-249.

Smith, T. B., & Skúli, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Annu. Rev. Ecol. Syst., 27, 111-133.

Snyder, N. F., Derrickson, S. R., Beissinger, S. R., Wiley, J. W., Smith, T. B., Toone, W. D., & Miller, B. 1996. Limitations of captive breeding in endangered species recovery. Cons. Biol., 10, 338-348.

Spurway, H. 1955. The causes of domestication: an attempt to integrate some ideas of Konrad Lorenz with evolution theory. J. Genetics, 53, 325-362.

Suomi, S. J., 1987. Genetic and maternal contributions to individual differences in rhesus monkey biobehavioral development. In: Perinatal Development: A Pshychobiological Perspective (Ed. by N. Krasnegor, E. Blass, M. Hofer, & W. Smotherman), pp. 397-419. Academic Press, New York.

Suomi, S. J., 1991. Uptight and laid-back monkeys: Individual differences in the response to social challenges. In: Plasticity of Development (Ed. by S. E. Brauth, W. S. Hall, & R. J. Dooling), pp. 27-56. MIT Press, Cambridge, Mass.

Svendsen, G. E. 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. Ecology, 55, 760-771.

Swain, D. P., & B. E. Riddell. 1989. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, Oncorhynchus kisutch. Can. J. Fish. Aquat. Sci., 47, 566-571.

Tully, J. J. & Huntingford, F. A. 1987. Parental care and the development of adaptive variation in anti-predator responses in sticklebacks. Anim. Behav., 35, 1570-1572.

Tully, J. J. & Huntingford, F. A. 1988. Additional information on the relationship between inter-specific aggression and anti-predator behaviour in the three-spined stickleback, Gasterosteus aculeatus. Ethology, 78, 219-222.

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, Wyoming, USA.

Varner, G. E., & Monroe, M. C.. 1991. Ethical perspectives on captive breeding: is it for the birds? Endangered Species Update, 8, 27-29.

Velleman, P. F., & Hoaglin, D. C. 1981. Applications, basics, and computing of exploratory data analysis. Duxbury Press, Boston.

Villablanca, F. X. 1996. Conservation genetics of the black-footed ferret I: a phylogenetic perspective. In: Abstracts of the American Society of Mammalogists 1996 Annual Meeting.

Vincent, R. E. 1960. Some influences of domestication upon three stocks of brook trout (Salvelinus fontinalis Mitchill). Trans. Amer. Fish. Soc., 89, 35-52.

Ward, J. F., Macdonald, D. W., Doncaster, C. P., & Mauget, C. 1996. Physiological response of the European hedgehog to predator and nonpredator odour. Physiol. & Behav., 60, 1469-1472.

Wcislo, W. T. 1989. Behavioral environments and evolutionary change. Ann. Rev. Ecol. Syst., 20, 137-169.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the orignis of diversity. Annu. Rev. Ecol. Syst., 20, 249-278.

Williams, E. S., Thorne, E. T., Appel, M. J. G., & Belitsky, D. W. 1988. Canine distemper in black-footed ferrets (Mustela nigripes) from Wyoming. J. Wildl. Dis., 24, 385-398.

Williams, E. S., Thorne, E. T., Kwiatkowski, D. R., Anderson, S. L., & Lutz, K. 1991. Reproductive biology and management of captive black-footed ferrets (Mustela nigripes). Zoo Biol., 10, 383-398.

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. 1994. Shyness and boldness in humans and other animals. Trends in Ecol. and Evol., 9, 442-446.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. 1993. Shy-bold continuum in pumpkinseed sunfish (Lepomis gibbosus): an ecological study of a psychological trait. J. Comp. Psych., 107, 250-260.

Wilson, D. S., & Yoshimura, J. 1994. On the coexistence of specialists and generalists. Amer. Nat., 144, 692-707.

Youngman, P. M. 1982. Distribution and systematics of the European mink, Mustela lutreola Linnaeus 1761. Acta Zool. Fennica 166, 1-48.

Table 2.1. Statistical summary of behavioural comparisons among generations 1, 3, and 4 of Siberian polecats, between black-footed ferrets (generations 3-5) and generation 1 polecats, and between black-footed ferrets and generation 4 polecats (H=Chi-square approximation for Kruskal-Wallace or Mann-Whitney test).

	Among Polecat Generations (d.f.=2)		Polecat (Gen. 1) vs. Ferret (d.f.=1)		Polecat (Gen. 4) vs. Ferret (d.f.=1)	
	H	P	H	P	H	P
Pre-attack measure:						
Latency to depart burrow cell	20·057	<0·001	3·030	0·082	14·362	<0·001
First departure to owl stoop	4·504	0·105	3·630	0·057	1·576	0·209
Time within cell	8·074	0·018	2·843	0·092	3·289	0·070
Time out of cell	8·465	0·015	8·000	0·005	1·490	0·222
Number of returns	10·780	0·005	7·592	0·006	1·397	0·237
Post-attack measure:						
Owl stoop to burrow descent	11·861	0·003	8·627	0·003	0·684	0·166
Descent to first post-owl departure	6·652	0·036	6·817	0·009	0·049	0·825

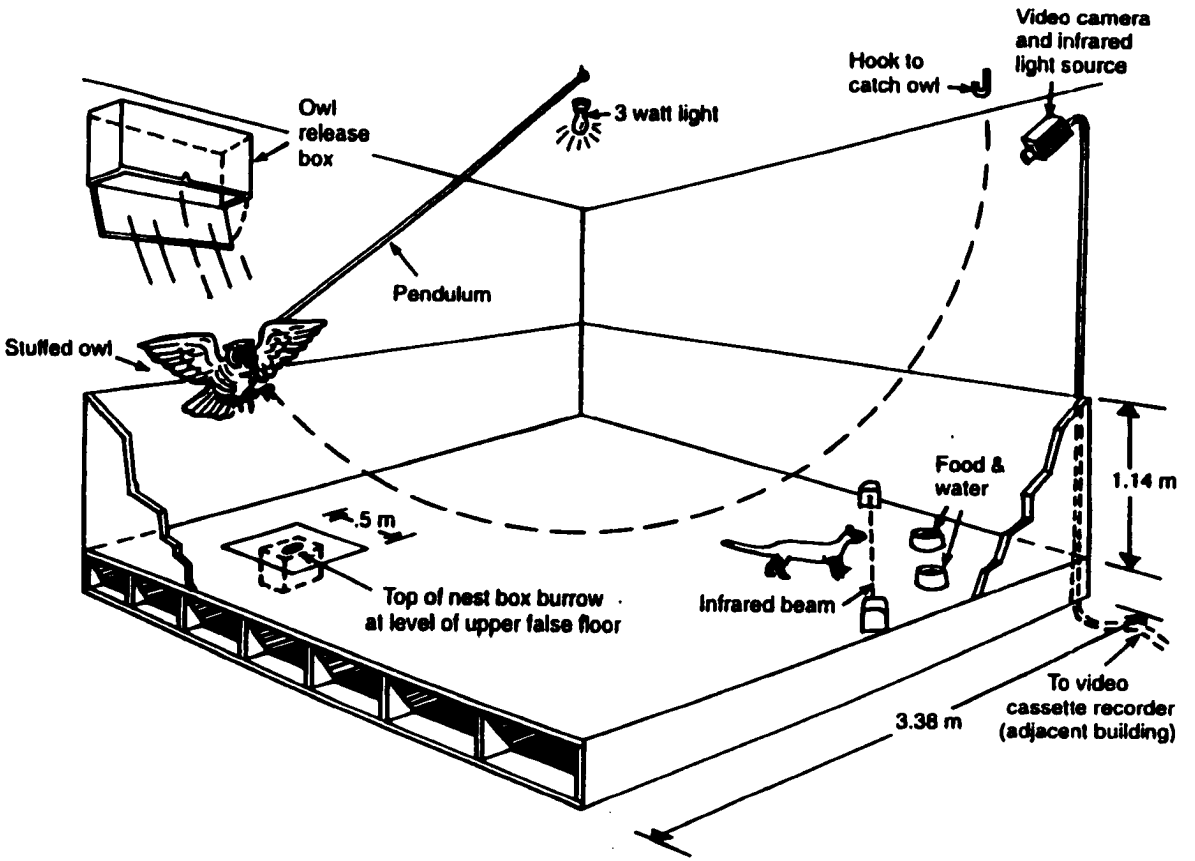

Figure 2.1. Oblique view of the shelter-field enclosure and owl release mechanism.

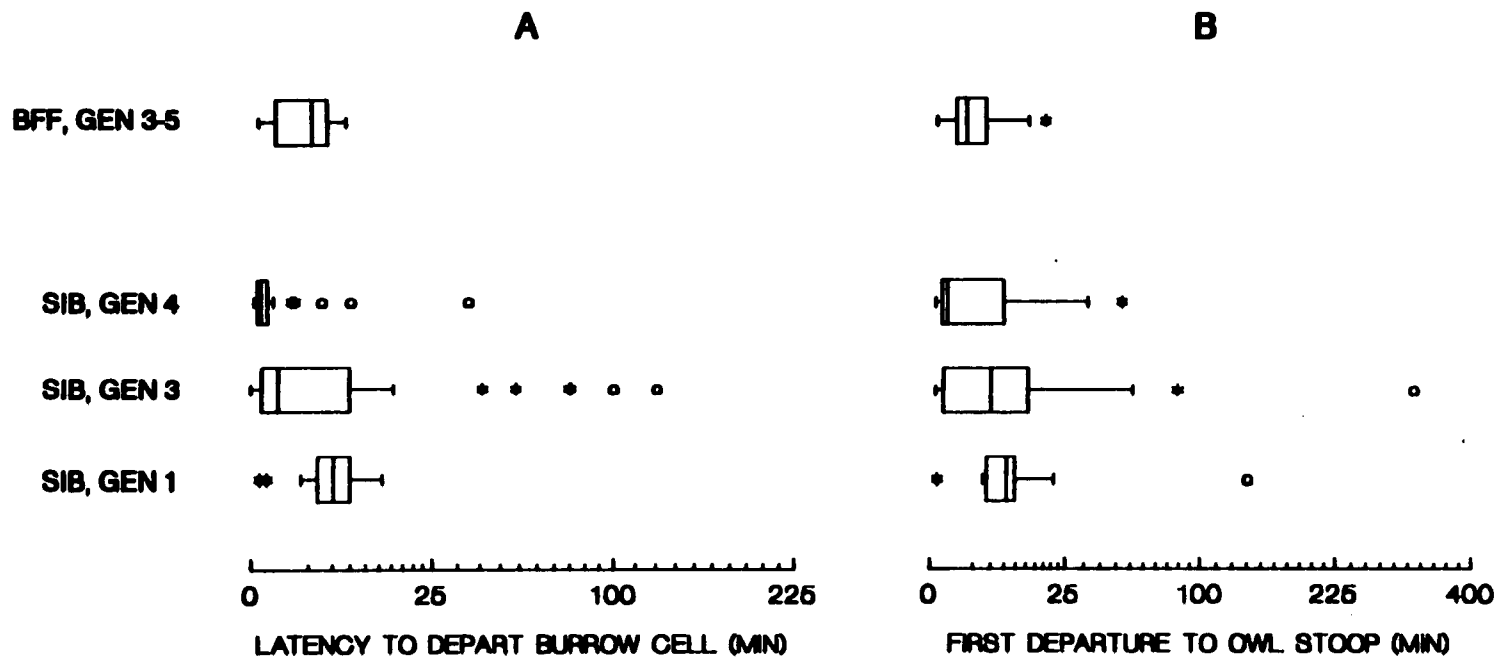

Figure 2.2. Durations of the two stages comprising the shelter-field exploration phase of trials. Measures are (A) minutes from the time subject was first visible in the "burrow" opening to the time of first departure from the 0·25 m^2 cell surrounding the burrow, and (B) minutes from that first departure to the time the owl's swing reached its lowest point. Box plots (Velleman and Hoaglin, 1981) indicate values of observations at the 25th and 75th percentiles (box), medians (line in box), range (whiskers), and outliers (*,o).

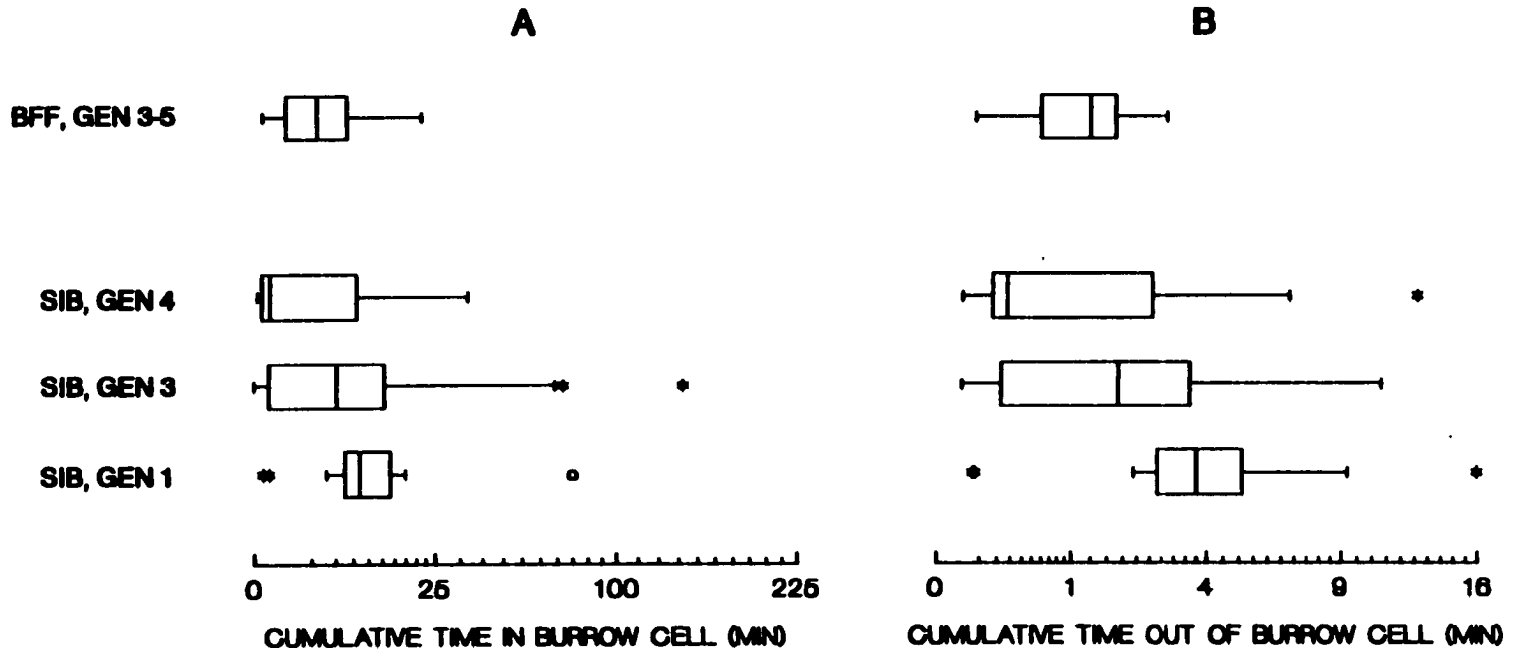

Figure 2.3. Cumulative time spent by subjects (A) within the 0·25 m^2 cell surrounding the burrow and (B) outside of the burrow cell during the shelter-field exploration phase of trials. Box plots (Velleman and Hoaglin, 1981) indicate values of observations at the 25th and 75th percentiles (box), medians (line in box), and range (whiskers), and outliers (*,○).

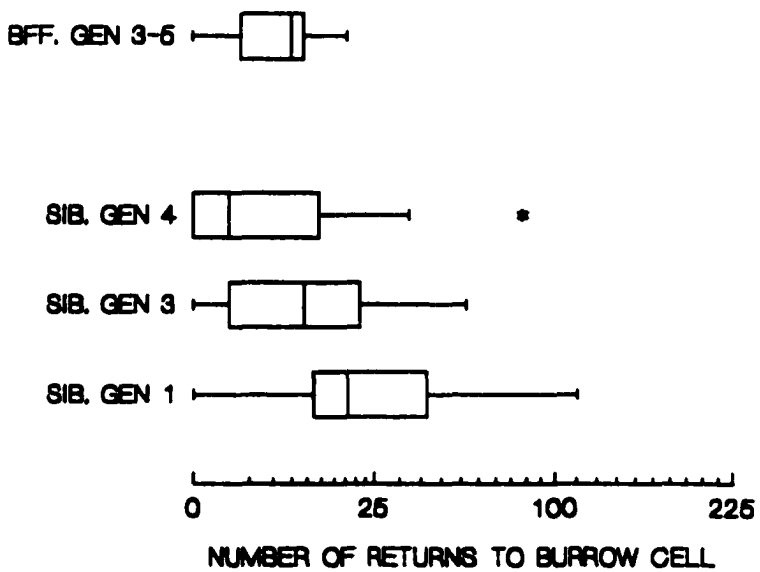

Figure 2.4. Number of occasions subject returned to the 0·25 m^2 cell surrounding the burrow during the shelter-field exploration phase of trials. Box plots (Velleman and Hoaglin, 1981) indicate values of observations at the 25th and 75th percentiles (box), medians (line in box), range (whiskers), and outliers (*,o).

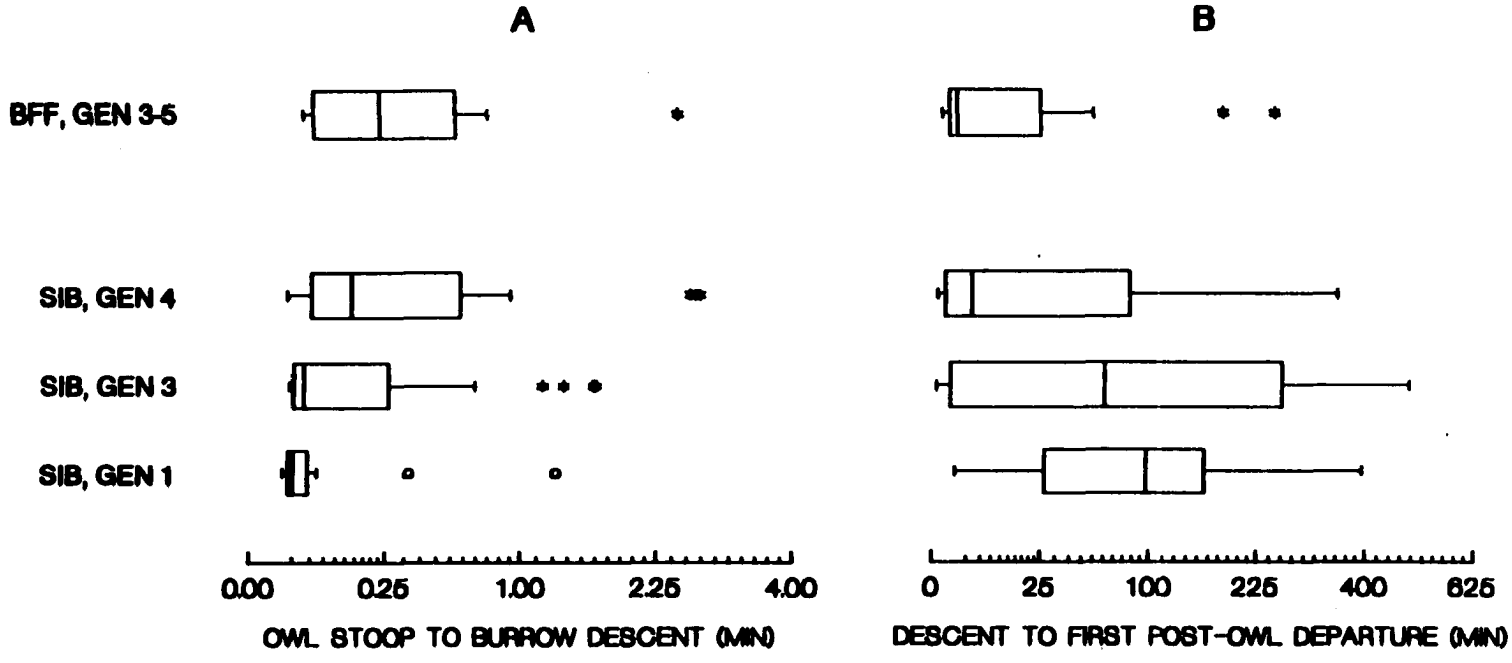

Figure 2.5. Durations of the two stages comprising the post-attack phase of trials. Measures are (A) minutes from the lowest point of owl swing to disappearance of subject into burrow, and (B) minutes from disappearance of subject into burrow to subjects' first post-attack departure from the 0·25 m^2 cell surrounding the burrow. Box plots (Velleman and Hoaglin, 1981) indicate values of observations at the 25th and 75th percentiles (box), medians (line in box), range (whiskers), and outliers (*,o).

CHAPTER 3

MORTALITY OF SIBERIAN POLECATS AND BLACK-FOOTED FERRETS DURING EXPERIMENTAL RELEASES ON PRAIRIE DOG COLONIES[1]

ABSTRACT

Black-footed ferrets (Mustela nigripes) likely were extirpated from the wild in 1985-86, and their repatriation depends on captive breeding and reintroduction. Post-release survival of animals may be effected by behavioral changes induced by captivity. We released neutered Siberian polecats (M. eversmannii), close relatives of ferrets, in 1989-90 on black-tailed prairie dog (Cynomys ludovicianus) colonies in Colorado and Wyoming to test rearing and reintroduction techniques. Captive-bred 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-caught polecats from China in 1990 and released cage-reared black-footed ferrets in 1991. We documented mortality for 55 of 92 radio-tagged animals in all studies, mostly due to predation (46 cases). Coyotes (Canis latrans) killed 31 ferrets and polecats. Supplementally fed polecats survived better ($P = 0.015$) than non-provisioned polecats. With a model based on deaths/distance moved, survival was highest for wild-born polecats, followed by pen-experienced, then

[1]Formatted for submission to *Journal of Mammalogy*

cage-reared groups ($P<0.001$). Indices of abundance (from spotlight surveys) for several predators were correlated with mortality rates of polecats and ferrets due to those predators ($R^2 = 0.707$, $P = 0.005$). Released black-footed ferrets had lower survival rates than their ancestral population in Wyoming ($P < 0.001$), and lower survival than wild-caught and translocated polecats ($P < 0.001$), emphasizing the influence of captivity. Captive-born polecats lost body mass more rapidly post-release than did captive-born ferrets ($P < 0.001$). Prey selection further emphasized species differences.

INTRODUCTION

To the best of our knowledge, black-footed ferrets (Mustela nigripes) were extirpated from the wild in 1985-1986, and their recovery depends on re-establishing free-ranging populations from captive-raised stock (U.S. Fish and Wildlife Service, 1988). Some types of investigations on black-footed ferrets have been precluded because of their rarity and legally endangered status. Siberian polecats (M. eversmannii), closely related to black-footed ferrets, 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). Black-footed ferrets and Siberian polecats have interbred and produced fertile offspring at the Wyoming captive breeding facility, supporting morphological (Anderson et al., 1986) and genetic evidence of relatedness (O'Brien et al., 1989). Our use of Siberian polecats in this early stage of the ferret repatriation process parallels the California condor (Gymnogyps californicus) program, with its research on the Andean condor (Vultur gryphus) (Wallace, 1989).

Relaxed natural selection (or artificial selection) and cultural changes during captivity can alter behavioral repertoires important to survival in the wild. Captive rearing conditions affect both behavioral and physical development (Beck et al., 1994; Caro, 1980; Clark and Galef, 1977; Derrickson and Snyder, 1992; Kleiman, 1989; Renner, 1988; Rozenzweig, 1979; Snyder et al., 1996). Coworkers and I have shown differences in development of predatory and anti-predator behaviors when Siberian polecats are raised under varying conditions and tested in the laboratory (Miller et al., 1990a,b).

In the present experiments, we released and radio-tracked 55 Siberian polecats during 1989--90 to test the effect of 5 different combinations of rearing and release methods on survival (Table 3.1), and as a pilot study to identify problems likely to occur during reintroductions of black-footed ferrets. We also radio-tracked 37 of the first black-footed ferrets released in 1991 as a pilot test of techniques. All black-footed ferrets were released using a single strategy, although the merits of comparative designs were debated (Biggins et al. 1997; Miller et al., 1996). Releases of black-footed ferrets and Siberian polecats under similar conditions enabled further evaluation of the ecological equivalence (Hoffmann and Pattie, 1968) of the two species.

METHODS

Study sites.--Success of released polecats and ferrets may 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 black-footed ferret release site with strip transects to characterize densities of total and active burrows. We estimated prairie dog densities from density of active burrows (Biggins et al., 1993).

The Veteran, Wyoming study site was a 250-ha black-tailed prairie dog (Cynomys ludovicianus) colony with an estimated 148 burrows/ha and about 23 prairie dogs/ha. Nearby colonies were small and separated widely. Other potential prey species were cottontail rabbits (Sylvilagus sp.), kangaroo rats (Dipodomys ordii), deer mice (Peromyscus maniculatus), and pocket gophers (Geomyidae, Geomys sp. or Thomomys sp.). Wild Siberian polecats hunt ecologically similar prey in their Asian habitat (Stroganov, 1962; Zheng et al., 1983). Government aerial gunners killed about 30 coyotes (Canis latrans) in 1989 on lands adjacent to the study site (Gordon Booth, pers. comm.). Prior to and during the period of the study, sport hunters on several occasions chased and killed coyotes on and near the study area using dogs.

The Hasty, Colorado study site was a 250-ha black-tailed prairie dog colony with 75 burrows/ha and about 11 prairie dogs per ha. Several other colonies (some of which were > 1000 ha) were nearby. Other prey species were similar to those at Veteran, but the geomyid was the yellow-faced pocket gopher (Cratogeomys castanops). Hay meadows, other croplands, and a riparian zone along the nearby Arkansas River created a more varied mix of habitats than at the other sites. The only predator control at this site was by sport hunting.

The release site for black-footed ferrets, in Shirley Basin, Wyoming was a 660-ha white-tailed prairie dog (Cynomys leucurus) colony with 82.7 active burrows/ha and about12 prairie dogs/ha (B. Oakleaf, E. Thorne, B. Luce, and B. Williams, 1991 Annual Report, Black-footed Ferret Reintroduction, Wyoming Game and Fish Department, Cheyenne). This colony was part of a complex with >20,000 ha in mapped colonies.

Several other colonies were within 1 km of the release colony. Prior to release of the black-footed 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 during the study.

Rearing.-- We translocated 5 wild-born Siberian polecats (M. e. dauricus) from eastern Inner Mongolia, China. These animals were quarantined in cages in China for at least 1 month prior to shipment, quarantined for an additional 40-62 d in cages in the U.S. prior to release, and received no pre-release conditioning. Captive-born Siberian polecats were produced at the National Zoo's Conservation and Research Center (CRC) from stock obtained from the Moscow Zoo, Russia, which stemmed from animals of unknown sub-species and origin. We cross-fostered polecats captive born in 1990 between pen reared and cage reared groups (Table 3.1) to distribute related individuals across both treatments.

Cage-reared ferrets and polecats were raised in 1.22m X 1.22m cages with attached nest boxes, and were fed commercial ferret ration and dead prairie dogs. Cage-reared polecats were held an additional 2 weeks at their release sites for acclimation to their new release cages.

We initially raised pen-experienced polecats in 2 m X 3 m cages until 3.5 months of age, then placed them into 2 pens (at the Pueblo Army Depot, Pueblo, Colorado, and at CRC), each having a semi-natural 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 before their release. Their food supply 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 which were released with their kits). We reproductively sterilized polecats at least 3 weeks before release, via removal of oviducts of females and the vasa deferentia and epididymides of males. We left ovaries and testes intact in an attempt to minimize impact on behaviors. Castrated male ferrets may have testosterone levels only 5 % of those sterilized with testes intact (Kastner and Apfelbach, 1987). We weighed polecats and ferrets before release and recaptured them periodically for re-weighing and to assess general condition.

We released ferrets and polecats that were not wild-caught or conditioned in outdoor pens from cages similar to their rearing cages (Table 3.1). The animals' natal nest boxes were attached to release cages. After 10-14 d of on-site acclimation, we opened a 12 cm diameter plastic tube extending from each cage floor to the ground, allowing animals to leave. We provided dead prairie dogs in the cage for 10 d post-release.

We released wild-caught 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 supplementally fed each group with portions of prairie dog at the time and burrow of release, and in other occupied burrows on d 3 and 8 post-release, except for 6 non-provisioned polecats that were released at Veteran in 1989 (Table 3.1).

Radio-telemetry.--A 10 g transmitter package with a 20 cm whip antenna was attached to a 100% wool collar 1 cm wide. The 2-stage, 3-volt transmitter had a motion-sensitive mercury switch that triggered changes in pulse rate, resulting in continuously variable pulse intervals ranging from 2.4 s for inactive animals to 0.9 s for rapidly moving animals. Battery life was about 40 d. We physically restrained animals (captive-raised polecats) or immobilized them with ketamine hydrochloride (wild-caught polecats and black-footed ferrets) for collaring, and glued overlapping ends of the wool collar with contact cement.

We monitored released ferrets and polecats (n=92) via radio-telemetry (Table 3.1). Twelve black-footed ferrets were intentionally released without transmitters in 1991, and a few black-footed ferrets and polecats were not radio-tracked due to lost collars or malfunctioning transmitters. Duration of radio-tracking varied from <1 d to 42 d. We accumulated 765.4 radio-days of telemetric monitoring during these studies (1 radio day = 1 radio-tagged animal monitored for 1 d). Cessation of tracking was primarily due to death of animals, collar loss, or loss of contact due to unknown causes, but we tracked a few animals until the end of each study (a minimum of 1 month postrelease).

Intensive monitoring was primarily by triangulation using methods developed for black-footed ferrets (Biggins et al., 1985). We monitored released animals from 3-4 modified camper trailers fitted with dual beam, 11-element, rotatable Yagi antennas mounted on 6.1-m masts, supplemented by 2 trucks fitted with smaller rotatable Yagi antennas (Chap. 4). We accurately surveyed station locations using standard land survey techniques. We tested angular accuracy of bearings from each fixed station by comparing

50-90 pairs of transit-derived and telemetry derived bearings to beacon transmitters (Biggins et al., 1999). At least 2 stations were in simultaneous operation for 16-24 hours/d, including all hours of darkness. We referenced stations using a multiple radio beacon procedure (Biggins et al., 1999). We field-processed referencing calculations and azimuth data from the stations using a laptop computer and program TRITEL (by Biggins). Computer output aided trackers in assessing accuracy of fixes, locations of animals, speed and direction of animal movements, and circumstances suggesting mortality. We estimated movements as cumulative straight-line distances between consecutive telemetric fixes, which were usually separated < 15 min. when animals were aboveground (Chap. 4). In addition, we used 3 receiver/strip chart recorder combinations for automatic acquisition of non-locational data depicting signal modulation and pulse interval (Chap. 4); 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 of mortality from combinations of telemetric evidence, evidence at the kill site (digging, tracks, scat, feathers, 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 "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 (some at depths > 2 m). In 2 cases, we could

not attribute deaths to predation or starvation; these cases were included in an analysis of overall mortality, but were not considered during separate analyses of predation and starvation.

Modeling mortality rate–general methods.–We assessed rates of predation on ferrets and polecats using maximum likelihood estimators for competing risk analysis. Program MICROMORT (Heisey and Fuller, 1985) produced estimates of survival and mortality, based on relating number of deaths to "radio-days" of monitoring. Daily survival rate ($\hat{s}_i$) during a time interval (i) is 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 with a length of L_i days is:

$$\hat{S}_i = \hat{s}_i^{L_i}$$

The method assumes a constant hazard rate to losses throughout the estimation interval, an assumption that is unlikely to be strictly met. That assumption, however, becomes more realistic if long time periods are subdivided into shorter periods. We used 2 intervals (release through d 3 postrelease and d 4-10 postrelease) as a starting point for most analyses. The method also assumes independence of each "animal-day," and our data appear to meet the criteria of Heisey and Fuller (1985). We derived rates of mortality solely from animals known to be dead; those rates, therefore, are minimum rates. Loss of telemetric contact with animals may have been due to collars lost too deeply underground for detection of a telemetric signal, to deaths occurring deep underground, or transmitters

that were crushed during attacks from large predators (we recovered several badly damaged transmitters).

Our intensity of telemetric monitoring allowed identification of time of death more accurately than the daily rate proposed by Heisey and Fuller (1985). We monitored status of aboveground animals closely, and on several occasions arrived at the scene minutes after predation occurred. Timing of belowground mortality was more difficult to determine, but could be classified into 8-h periods. We thus used 8 h or 12 h periods for analyses. Choice of period length affects mortality estimates because animals that die are assumed to be alive only at the beginning of a period. The effect of that bias on our comparative analyses is expected to be small because bias is reduced by our short classification periods (compared to examples of Heisey and Fuller ,1985), and that bias should be distributed equally among our treatments.

Much of the risk of predation for ferrets and polecats is associated with movement aboveground. 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/time, but in the survival analyses "radio-meters" (the base measure was deaths/100 m of movement) was substituted for "radio-days" of the time-based procedure. For this distance-based measure, badger predation was not considered because it occurred belowground at polecat and ferret resting sites.

Likelihood ratio tests assisted in selection of the most parsimonious nested submodel explaining significant variation. Parenthetical chi-square 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 accurately estimate survival rates per se (Labreton et al., 1992).

Surveys of predators and alternative prey.–We counted nocturnal predators and small mammals while spotlighting from a vehicle at about 1 h after sunset and at midnight, using a 300,000 candle power light. Pre-established 5.2- km routes traversed the experimental prairie dog colonies. These surveys at Shirley Basin occurred after most predator control was completed.

Risk of predation on Siberian polecats and black-footed ferrets may depend partly on their encounter rates with large predators. Assuming random movements in space and time by prey and predators, a simple model predicts a linear increase in hazard rate of predation with an increase in predator density. Sighting rates (numbers of predators/h) were compared with predator-specific mortality rates for polecats and ferrets at those sites (from the MICROMORT estimates), using linear regression analysis.

Effect of rearing and release methods.--Because of the unbalanced overall design (Table 3.1), we used different, non-independent, subsets of polecat data to optimize balance and sample size for each evaluation. No cells were empty for these comparisons. We compared burrow releases with and without supplemental provisioning within the 1989 Veteran dataset, using the time-based survival model. We compared the Hasty and Veteran sites within sexes and 2 rearing-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 examine cage-reared and released vs. pen-reared and burrow-released groups of captive-born polecats, comparing these groups within males at Veteran, and within females at Hasty and Veteran, again with both time-based and distance-based estimates of mortality.

Predation and starvation.--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 (separated at 3-d postrelease). We separately characterized predation and starvation for ferrets, for polecats at both Hasty and Veteran, and for sexes of both species. We pooled polecat rearing/release groups into a large subset containing all captive-reared animals, but retained identity of the two sites.

Body mass.--We weighed animals (using a spring scale) to the nearest 10 g, at the time of radio-collaring before release, when they were recaptured for collar replacement or for inspections of overall condition, and when they were recaptured during spotlight surveys to assess survival (Chap. 5). For a few animals, we weighed intact remains. We used multiple regression 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. Model selection began with the most general model (as with mortality analyses), which was reduced by sequential deletion of variables that appeared non-significant ($P < 0.05$).

Captive-born and wild-born polecats and ferrets.--We compared survival of the captive-reared black-footed ferrets released at Shirley Basin, Wyoming in 1991 to survival of radio-tagged ferrets monitored in the wild population at Meeteetse, Wyoming (from data summarized by Forrest et al., 1988), using a simple, 2-parameter general model (wild

and captive) contrasted with a reduced model with pooled rearing categories. We made a similar comparison between captive-reared black-footed ferrets and the wild-born Siberian polecats from China. Both groups were translocated, unlike the Meeteetse ferrets.

RESULTS

Radio-tracking from fixed stations produced 5662 locational estimates from which we calculated interfix estimates of movement. Additional non-locational data from technician-occupied stations (4571 data lines) and from automated equipment assisted in determining status (alive or dead) and timing of mortality. We detected 55 cases of mortality (Table 3.2), mostly due to predation by coyotes (31 cases). Overall survival rates of captive-reared animals were highly variable among sites (Table 3.3).

Badgers ate their ferret and polecat kills. Remains, often just the radio-collar, 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 may 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 polecats were coiled and covered by soil and ground litter. Radio-tagged polecats left in 3 cache sites at Veteran for 4, 6, and 9 d 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/or radio collar 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 after the motion sensitive transmitters suggested predation, and saw coyotes retreating from the remains as we approached.

Two known polecat deaths were due to avian predators. A great horned owl caused the only known death of a wild-caught polecat, and that was the only death in any of the groups due to an owl (the polecat was consumed). A polecat also was killed by an unidentified diurnal raptor.

The 2 polecats that survived longest (about 5 d) at Hasty were wild-caught; 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. A 510 g dead pocket gopher was recovered from a burrow 10 m from the last known location of the polecat. Two of the longest survivors (1 pen-experienced and 1 wild-caught) at Veteran also moved away from the prairie dog colony and occupied pocket gopher burrows, but the only prey known to have been taken was a cottontail.

The high density of predators at Hasty 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 pre-release acclimation period, a golden eagle (Aquila chrysaetos) was once flushed from the ground within a few m of an occupied cage.

Surveys of predators and alternative prey.–Sighting rates for all predators combined (Table 3.4) were highest at Hasty (2.75/h), intermediate at Veteran (0.90/h), and lowest at Shirley Basin (0.44/h), and differed significantly among the 3 sites (Kruskal-Wallis, $\underline{X}^2$ approximation = 13.70, $\underline{d.f.}$ = 2, $\underline{P}$ = 0.001). Alternative prey species (leporids and Dipodomys ordii) were not surveyed at Shirley Basin, but sighting rates for these species combined were significantly higher at Hasty than at Veteran ($\underline{X}^2$ approximation = 13.52, $\underline{d.f.}$ = 1, $\underline{P}$ < 0.001). Kangaroo rats are a potential prey item, but polecats were not known to have taken them during this study. Although a 10-fold higher density of leporids at Hasty may have provided the polecats with additional prey, it may also help explain the high density of coyotes at that site. Square root transformation of the predator sighting rate and mortality rate data (Fig. 3.1) resulted in improved normality and homoscedasticity of residuals. Transformed sighting rates for coyotes, badgers and great horned owls were correlated with mortality rates of ferrets and polecats attributable to those 3 predators ($\underline{R}^2$ = 0.707; $\underline{F}$ = 16.896; $\underline{d.f.}$ = 1,7; $\underline{P}$ = 0.005) (Fig. 3.1).

Effect of rearing and release methods.--For the test of supplemental provisioning done in 1989, the overall daily mortality rate of the supplemented polecats ($1-\hat{S}_i$ = 0.0924) was lower than the mortality rate for unsupplemented polecats ($1-\hat{S}_i$ = 0.3333), as implied by the significant difference between the general model (2 parameters) and reduced model (1 parameter resulting from pooled provisioning categories) ($\underline{X}^2$ = 5.91, $\underline{d.f.}$ = 1, $\underline{P}$ = 0.015). Moreover, supplemental provisioning seemed to reduce the rate of predation. Daily mortality rates due to predation also were lower for the supplemented group ($1-\hat{S}_i$ = 0.1109) compared to the unsupplemented group ($1-\hat{S}_i$ = 0.4000), again via

a contrast of 2-parameter general and 1-parameter reduced models ($X^2 = 4.71$, d.f. = 1, P = 0.030).

Using a restricted subset of data with captive-reared polecats of both sexes, site (Hasty vs. Veteran) was a significant covariate in both the time-based model (general model with 2 sexes X 2 rearing/release groups X 2 sites compared to reduced model with 2 sexes X 2 rearing/release categories and pooled sites; $X^2 = 43.0$, d.f. = 4, $P<0.001$) and the distance-based (models as above; $X^2 = 32.9$, d.f. = 4, $P < 0.001$) model of mortality rate (Fig. 3.2), 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/release appeared to effect time-based survival estimates (general model with 2 sites X 3 rearing/release groups compared to reduced model with 2 sites and pooled rearing categories; $X^2 = 14.1$, d.f. = 4, $P = 0.007$) and distance-based survival estimates (models as above; $X^2 = 23.9$, d.f. = 4, $P < 0.001$). 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. 3.2), general models (2 rearing/release groups X 3 sites/sexes) were not different from reduced models (3 sites/sexes and pooled rearing groups) for either time-based survival estimates ($X^2 = 4.7$, d.f. = 3, $P = 0.195$) or distance-based estimates ($X^2 = 3.7$, d.f. = 3, $P=0.296$). Much of the overall difference in the 3-group comparison, therefore, appears to be due to the wild-born polecats, but the

intermediate survival of the pen-reared group using the distance-based model (Fig. 3.2) suggests pen experience is beneficial.

Pen-raised polecats practiced hunting and killing prairie dogs in captivity, but there was no evidence they were able to kill free-ranging prairie dogs. Wild-caught polecats made no attempt to kill live prairie dogs in captivity, although they fed on prairie dog carcasses and they killed kangaroo rats and other small mammals. We witnessed 1 aboveground encounter between a wild-caught 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, while the third was initiated by the prairie dog. After the third bout, both animals retreated to separate burrows.

Predation and starvation.--Because captive-reared animals released at Hasty did not survive > 3 d, and because starvation at all sites occurred after 3 d postrelease, separation of time periods was considered important and further analyses were conducted separately for the period 0-3 d postrelease and the period 4-10 d postrelease. The initial dataset involved captive-reared polecats and ferrets from all release sites. General statistical models of predation and starvation for the first 3 d had 6 parameters (2 sexes X 3 sites); the deletion of data from Hasty resulted in 4-parameter models for the 4-10 d period.

In all studies, only 6 animals were classified as having starved, of which 3 resulted in death; those 3 animals lost 33-40% of their body mass, and survived 12-14 d after the last known feeding. There was no evidence for different starvation rates due to sex, site,

or species; reduced models pooling sexes or species/sites were not significantly different from the general model (sexes, $\underline{X}^2 = 1.20$, $\underline{d.f.} = 2$, $\underline{P} = 0.549$; sites-species, $\underline{X}^2 = 0.82$, $\underline{d.f.} = 2$, $\underline{P} = 0.664$). Predation rates, however, seemed lower for captive-reared black-footed ferrets than for captive-reared Siberian polecats (although species and site are confounded), and were lower for males than for females (Fig. 3.3); all pooled submodels were significantly different from their respective general models during the first 3 d postrelease (pooling sexes, $\underline{X}^2 = 8.0$, $\underline{d.f.} = 3$, $\underline{P} = 0.046$; pooling species/sites, $\underline{X}^2 = 48.6$, $\underline{d.f.} = 4$, $\underline{P} < 0.001$) and during d 4-10 postrelease (pooling sexes, $\underline{X}^2 = 7.9$, $\underline{d.f.} = 2$, $\underline{P} = 0.019$; pooling species/sites, $\underline{X}^2 = 24.5$, $\underline{d.f.} = 2$, $\underline{P} < 0.001$).

Body mass.--In the general regression model of change in mass (predictors = species, sexes, days postrelease and all interactions), the interaction of time and species was highly significant ($\underline{F} = 18.36$; $\underline{d.f.} = 1,42$; $\underline{P} < 0.001$). We thus chose to segregate species for further analyses. For captive-born Siberian polecats, average masses at the time of release were 784 g for females and 1382 g for males; masses at release for translocated wild-caught polecats were 693 g for females and 860 g for the lone male. There was no detectable effect of sex on change in mass for all polecats combined ($\underline{F}=2.149$; $\underline{d.f.} = 1,16$; $\underline{P} = 0.162$), and the interaction between sex and time was not significant ($\underline{F} = 1.223$; $\underline{d.f.} = 1,16$; $\underline{P} = 0.284$) (Fig. 3.4A). The sole remaining predictor, days postrelease, was highly significant in the 2-parameter model ($\underline{F} = 52.51$; $\underline{d.f.} = 1,18$; $\underline{P} < 0.001$). Siberian polecats typically lost 1.7 % of their initial body mass per d postrelease.

Male and female black-footed ferrets responded differently from each other (interaction of days postrelease and sex in a 4-parameter model; $\underline{F} = 7.634$; $\underline{d.f.} = 1,25$; $\underline{P}$

= 0.011) in changes of mass over time (Fig. 3.4B). We thus assessed the sexes separately. Male ferrets (average mass at release = 926 g) tended to maintain their mass over time (2-parameter model; $\underline{F} = 0.553$; $\underline{d.f.} = 1,12$; $\underline{P} = 0.471$). Although their changes in mass were less dramatic than those of polecats, female ferrets (average mass at release = 757 g) lost mass at a significant rate of 0.6 % per d postrelease (2-parameter model; $\underline{F} = 8.720$; $\underline{d.f.} = 1,13$; $\underline{P} = 0.011$) .

Captive-born and wild-born polecats and ferrets.--The estimated 10-d survival for wild-born polecats (88%) was higher than for released black-footed ferrets (51%). The species were compared using a model that controlled for sex ($\underline{X}^2 = 13.11$, $\underline{d.f.} = 2$, $\underline{P} < 0.001$). The survival rate for released black-footed ferrets (49% for 1 month) was lower than ($\underline{X}^2 = 14.4$, $\underline{d.f.} = 1$, $\underline{P} < 0.001$) survival for free-ranging wild ferrets (93% for 1 month, from a dataset summarized by Forrest et al. 1988) 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. In contrast, the relatively low mortality rate of about 7%/month for free-ranging ferrets at Meeteetse (Forrest et al., 1988) did not suggest the high potential for predation experienced by our released polecats and ferrets, whose antipredator defenses appear compromised by captive-breeding and translocation. These results underscore a tenet of Lima and Dill (1990, p. 634): observed predation rates may not be good indicators of potential risk because "...antipredator behavior may be so effective that predators are rarely successful."

Mustela spp. have been documented as prey frequently (references in King, 1990; Korpimaki and Norrdahl, 1989a), but relatively little information exists concerning predation on non-reintroduced populations of black-footed ferrets (Forrest et al., 1988; Henderson et al., 1974; Sperry, 1941) and Siberian polecats (Kydyrbaev, 1988). Most investigations have concentrated on other aspects of Mustela biology. King (1990), for example, devotes 3 chapters to weasel (Mustela spp.) foods and hunting efficiency, but discusses their predators in 5 pages of the "Populations" chapter. In her reference section, 4 titles of 317 appear devoted to predation on weasels, compared to 61 titles related to predation by weasels. King (1990) was unconvinced that predation influenced density of weasels. In Kazakhstan, food habits studies of predators demonstrated predation on Siberian polecats by 4 mammalian predators and 1 avian predator, but predators were not thought to influence polecat populations (Kydyrbaev, 1988). Weasel abundance, however, was inversely related to fox (Vulpes and Urocyon) abundance (Latham, 1952; Mulder, 1990) and pine marten (Martes martes) abundance (Lindström et al., 1995). Powell's (1973) model suggested that predation sometimes limited weasel populations, and Korpicmaki and Norrdahl (1989a,b) suggested that avian predators may control weasel populations.

Predation has caused natural selection to favor morphological adaptations, including white winter pelage and black-tipped tails of northern weasels (King, 1990; Powell, 1982), but its effect on other physical attributes of Mustela remains speculative. The heavy predation rates of our study emphasize the potential selective effect on ferrets and polecats exhibiting maladaptive behaviors.

The rapid mortality due to coyote predation at Hasty argues for the theory of competing risks. Polecats were killed so quickly they had no time to starve. High density of prey (sciurids, murids, and leporids) and mid-sized predators at Hasty underscores a potential trade-off with high prey abundance for Mustela spp. With high prey density, energetic requirements are more easily met by Mustela spp., their reproductive success may be improved, and their risk of predation may be lower due to reduced time spent hunting aboveground and to their better body condition. High prey density, however, may result in a behavioral or numerical response (Holling, 1959) of generalist mid-sized predators, increasing their encounter rate with the Mustela. By taking prey nearly as large as themselves, and occupying the retreats of their prey, ferrets and polecats, like weasels (Korpimaki and Norrdahl, 1989a,b), are vulnerable to opportunistic attack by mid-sized predators hunting the abundant prey that has attracted both classes of predators. One important potential outcome is lack of density dependence in the relationship between Mustela and their predators. Mid-sized generalist predators are likely to respond (behaviorally or numerically) in a density dependent manner to the prey irrespective of the density of the Mustela spp.; the hazard rate for ferrets and polecats thus may be determined by the density of their prey rather than their own density. Mid-sized predators likely kill ferrets and polecats as incidental prey rather than a primary food source, and therefore are unlikely to respond directly to ferret or polecat density.

Predation rates of black-footed ferrets in our study seemed generally to decline over time. As animals with deficient skills are killed, the average fitness within the remaining cohort may increase. This cohort effect, in addition to increased survival skills

as animals learn about their new environment, may help explain the change in rate. Because polecats and ferrets were not released at the same site, species and site effects are confounded in our comparisons of survival of captive-reared animals. The lower index of abundance for predators at Shirley Basin and the relationship between mortality and that index support site differences as a possible explanation for the lower mortality rate of ferrets compared to polecats.

Although the confounding of site and species hampers interpretation, the higher survival for wild-born polecats (88 % for the first 10 d) compared to black-footed ferrets (51% for the first 10 d) is remarkable given the following circumstances: (1) 2 of the 5 polecats were released at Hasty, where predators were abundant and predation rates on polecats were high, (2) females, the sex with consistently lower survival rate during these studies, comprised 80% of the wild-born polecat sample but only 37% of the black-footed ferret sample, and (3) polecats were released onto black-footed ferret habitat. This, and the 93% monthly survival rate for wild-born black-footed ferrets at Meeteetse, Wyoming (Forrest et al., 1988) compared to the 49% monthly survival rate of captive-raised ferrets released at Shirley Basin, suggests an overwhelming effect 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 (Chaps. 2, 5) may not be fully overcome in a single generation by giving animals experience in a more natural environment. Our polecats, however, were transferred to pens when 120 d old. Black-footed ferrets kits reared in outdoor pens from 60 d survived dramatically better than cage-reared kits (Chap. 5). Transfer of young kits to pens presumably exposed them to

natural stimuli (burrows as home sites, prairie dogs as food, etc.) during sensitive periods for learning. Other potential benefits include opportunity for habituation to non-threatening stimuli (Shalter, 1984), reduced habituation to humans, and refinement of hunting and killing skills (Chap. 5).

The cage-release 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, Biggins et al. 1993). While using cages, the animals had unlimited access to water, but free water probably was not available after release. Thus, part of the post-release change in body mass may have been due to change in water balance. Because rates of mortality per km moved tended to be higher for cage-released animals than for pen-reared/burrow-released animals, advantages of post-release support seem superficial. Release cages may encourage sedentary behavior by providing shelter, food and water. Reduced activity may temporarily reduce risk of predation, but longer term success will require aboveground forays to hunt, to gain familiarity with their habitat, and interact with conspecifics.

Although burrow releases with supplemental provisioning have not been tested on black-footed ferrets, ferrets may benefit less than our polecats 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 (unpublished data), a phenomenon that is likely to have increased the predation rate for the provisioned group and may pose a similar problem if in-burrow provisioning were used for black-footed ferrets.

Perhaps the male black-footed ferrets of our 1991 study, which were about 22% larger than the females of that cohort, could kill prairie dogs more easily than females. Equal degradation of killing skills resulting from captivity thus may have greater impact on females than on males, a plausible explanation for the intersexual difference in change of mass. Wild and captive black-footed ferrets routinely kill prairie dogs (Campbell et al., 1987; Vargas, 1994), but injuries we have noticed in pen-raised black-footed ferrets and in free-ranging wild ferrets suggest prairie dogs, about equal in size to these polecats and ferrets, are not easy prey. Prairie dogs in their home burrows may have effective defenses against intra-burrow predation.

Two additional factors may have influenced the intersexual difference in change of mass for black-footed ferrets. Male and female wild-born Meeteetse ferrets at about 126 d of age were ca. 900 g and 700 g respectively (data extrapolated from Fig. 3 of Forrest et al., 1988), compared to the 926 g and 757 g mean masses of male and female ferrets released in 1991 at that age. Perhaps the released females tended to be more obese than the males at the time of release, and were simply losing excess fat. However, wild-born females had just 7.5 % less mass than captive-born females before their release, compared to about 20 % post-release loss in mass for captive-born females. Also, young males tend to reach adult size later than females (Vargas, 1994), and are 95 % of adult mass at 126 d of age, compared to females which are 99 % of adult mass at that age. Males thus demonstrated an expected pattern of slow gain in mass after their release (Fig. 3.4).

The greater tendency for starvation and significantly greater loss of body mass of captive-born polecats compared to black-footed ferrets suggests Siberian polecats were

not well-adapted to killing prairie dogs as prey. Pocket gophers, presumably taken by polecats during these studies, are ecologically similar to zokors (Myospalax spp.) found in Asia. Polecats were observed to dig into zokor burrows in Inner Mongolia (Biggins, unpublished data), and zokors (Myospalax fontanierii) are important polecat prey in Qinghai province, China (Zheng et al., 1983). Sciurid and murid rodents, and ochotonids are well represented in the diet of the Siberian polecats over their Eurasian range (Denisov, 1984; Gorbunov, 1983; Kydyrbaev, 1988; Peshkov, 1954; Stroganov, 1962; Zheng et al., 1983). Siberian polecats may be prey or habitat generalists (Erickson, 1973; Forrest et al., 1988) in the sense of taking a wide variety of prey over their large Asian range, but may specialize locally or regionally, and apparently cannot adapt quickly to all prey species taken by other Mustela spp. The term "ecological equivalent" (Hoffmann and Pattie, 1968) needs concise definition when applied to black-footed ferrets and Siberian polecats. Evidence from these releases suggests differences that may prevent either form from successfully invading habitat of the other.

The correlation of sighting rates for predators and mortality caused by those species should be interpreted cautiously because of the following: (1) if risks are competing (e.g. decreasing badger predation at a site increases the rate of predation by coyotes), response observations are not independent as assumed in regression analysis, (2) polecat and ferret vulnerability to predation likely differs, and (3) predator species are probably not equally detectable. Nevertheless, these correlational data suggest that attention be paid to densities of predators at future reintroduction sites for black-footed ferrets. Short-term predator control may be useful during initial phases of black-footed

ferret reintroductions. Even if their term in captivity has not resulted in loss of wariness, ferrets released into unfamiliar terrain will be at increased risk until they learn vital information about their new habitat. Reducing the abundance of the most important predators may partly compensate for initially high ferret vulnerability. Evidence for a statistically significant effect of predator density on ferret survival, however, does not necessarily imply a large biological effect (or the need for long-term predator control at reintroduction sites). Other factors, such as the effect of pre-release experience and habitat quality (Chap. 5) may be more important.

LITERATURE CITED

Beck, B. B., L. G. Rapaport, M. R. S. Price, and A. C. Wilson. 1994. Reintroduction of Captive-Born Animals. Pp. 265-286 in P. Olney, G. Mace, and A. Feistner, editors. Creative conservation: interactive management of wild and captive animals. Chapman and Hall, London, United Kingdom.

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.

Biggins, D. E., B. J. Miller, T. W. Clark, and R. P. Reading. 1997. Management of an endangered species: the black-footed ferret. Pp. 420-426 in G. K. Meffe and C. R. Carroll, eds., Principles of Conservation Biology, Second Edition. Sinauer Associates, Sunderland, Massachusetts.

_____, M. H. Schroeder, S. C. Forrest, and L. Richardson. 1985. Movements and habitat relationships of radio-tagged black-footed ferrets. Pp. 11.1-11.17 in S. H. Anderson and D. B. Inkley, eds., Proceedings of the Black-footed Ferret Workshop, 18-19 Sep. 1984. Wyoming Game and Fish Dept., Cheyenne. 228 pp.

_____, B. J. Miller, L. R. Hanebury, B. Oakleaf, A. H. Farmer, R. Crete, and A. Dood. 1993. A technique for evaluating black-footed ferret habitat. Pp. 73-87 in J. Oldemeyer, D. Biggins, and B. Miller, eds., Management of Prairie Dog Complexes for the Reintroduction of the Black-footed Ferret. U.S. Fish and Wildlife Service Biological Report 93-13, Washington, D.C.

Campbell, T. M., T. C. Clark, L. Richardson, S. C. Forrest, and B. Houston. 1987. Food habits of Wyoming black-footed ferrets. American Midland Naturalist 117: 208-210.

Caro, T. M. 1980. The effects of experience on the predatory patterns of cats. Behavioural and Neural Biology 29:1-28.

Clark, M. M., and B. G. Galef. 1977. The role of the physical rearing environment of the Mongolian gerbil (Meriones unguiculatus). Animal Behaviour 25:298-316.

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 Hauk. 15:89-93.

Derrickson, S. R., and N. F. R. Snyder. 1992. Potentials and limits of captive breeding in parrot conservation. Pp. 133-163 in S. R. Beissinger and N. F. R. Snyder (eds.), New World Parrots in Crisis: Solutions from Conservation Biology. Smithsonian Institution Press, Washington, D.C.

Erickson, R.C. 1973. Some Black-footed ferret research needs. Pp. 153-164 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop. South Dakota State Univ., Brookings. 208 pp.

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

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. South Dakota Department of Game, Fish and Parks Technical Bulletin #4.

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. 133 pp.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Journal of Entomology 91:385-398.

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. 1990. The natural history of weasels and stoats. Cornell University Press. Ithaca, New York. 253 pp.

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.

_____, and _____. 1989b. Avian predation on mustelids in Europe 2: impact on small mustelid and microtine dynamics--a hypothesis. Oikos 55;273-276.

Kydyrbaev, K. K. 1988. Ecology and behavior of mammals of Kazakhstan. Transactions of the Institute of Zoology, Academy of Sciences of Kazakh SSR 44:56-68.

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.

Lindström, E. R., S. M. Brainerd, J. O. Helldin, and K. Overskaug. 1995. Pine marten-red fox interactions: a case of intraguild predation. Ann. Zool. 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., D. Biggins, C. Wemmer, R. Powell, L. Hanebury, D. Horn, and A. Vargas. 1990a. Development of survival skills in captive-raised Siberian polecats (Mustela eversmanni) I: locating prey. Journal of Ethology 8:89-94.

_____, _____, _____, _____, L. Calvo, L. Hanebury, and T. Wharton. 1990b. Development of survival skills in captive-raised Siberian polecats (Mustela eversmanni) II: predator avoidance. Journal of Ethology 8:95-104.

_____, R. Reading, and S. Forrest. 1996. Prairie night--black-footed ferrets and the recovery of endangered species. Smithsonian Press, Washington, D.C., USA.

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.

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. Pages 21-33 in Conservation biology and the black-footed ferret. Yale University Press, New Haven, CT.

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.

_____. 1982. Evolution of black-tipped tails in weasels: predator confusion. American Naturalist 119:126-131.

_____, 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.

Renner, M. J. 1988. Learning during exploration: the role of behavioral topography during exploration in determining subsequent adaptive behavior. International Journal of Comparative Psychology 2:43-56.

Rosenzweig, M. R. 1979. Responsiveness of brain size to individual experience: behavioral and evolutionary implications. Pages 263-294 in M.E. Hahn, C. Jensen, and B.C. Dudek, editors. Development and evolution of brain size: behavioral implications. Academic Press, New York, New York, USA.

Shalter, M. D. 1984. Predator-prey behavior and habituation. Pp. 349-391 in Peeke, H. V. S. and L. Petrinovich, eds. Habituation, Sensitization, and Behavior. Academic Press, New York.

Snyder, N. F. R., and S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. Conservation Biology 10:338-348.

Sperry, C. G. 1941. Food habits of the coyote. U.S.D.I., 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. U.S. Dept. Commerce, Clearinghouse for Federal Scientific and Technical Information, Springfield, Virginia 22151.

U.S. Fish and Wildlife Service. 1988. Black-footed ferret recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado. 154 pp.

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

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(1):35-46.

Table 3.1. Number of Siberian polecats and black-footed ferrets monitored via radio telemetry to assess cause-specific mortality rates.

Species	Site and Year	Rearing & Release Method: Rearing ◊ Release ◊ Provisioning	Cage Burrow Unfed	Cage Burrow Fed[a]	Cage Cage Fed	Pen Burrow Fed	Wild Burrow Fed
Siberian Polecat	Veteran Wyoming 1989		6	7			
Siberian Polecat	Veteran Wyoming 1990				8	18	3
Siberian Polecat	Hasty Colorado 1990				6	5	2
Black-footed Ferret	Shirley Basin Wyoming 1991				37		

[a]animals provided with supplemental food after release

Table 3.2. Number of deaths of radio-tagged Siberian polecats and black-footed ferrets due to various causes.

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

[a]unknown cause and diurnal bird of prey
[b]great horned owl
[c]golden eagle

Table 3.3. Overall estimates of maximum daily survival and minimum daily mortality for captive-reared Siberian polecats and black-footed ferrets released onto prairie dog colonies. Daily rates are calculated for the first 10 d postrelease.

	Daily Rates			
	Survival (SD)	Mortality Due To:		
		Coyote	Badger	Other
Siberian Polecat Veteran, Wyoming 1989-90	0.88666 (0.01803)	0.04857	0.03886	0.02591
Siberian Polecat Hasty, Colorado 1990	0.15886 (0.09126)	0.84113	0.00000	0.00000
Black-footed Ferret Shirley Basin, Wyoming 1991	0.97642 (0.00777)	0.01310	0.00262	0.00786

Table 3.4. Sighting rates for predators and alternative prey species along nocturnal survey routes.

Site Year	Surveys (n)	Sightings/Hour				
		Coyote	Badger	Great Horned Owl	Hare & 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	

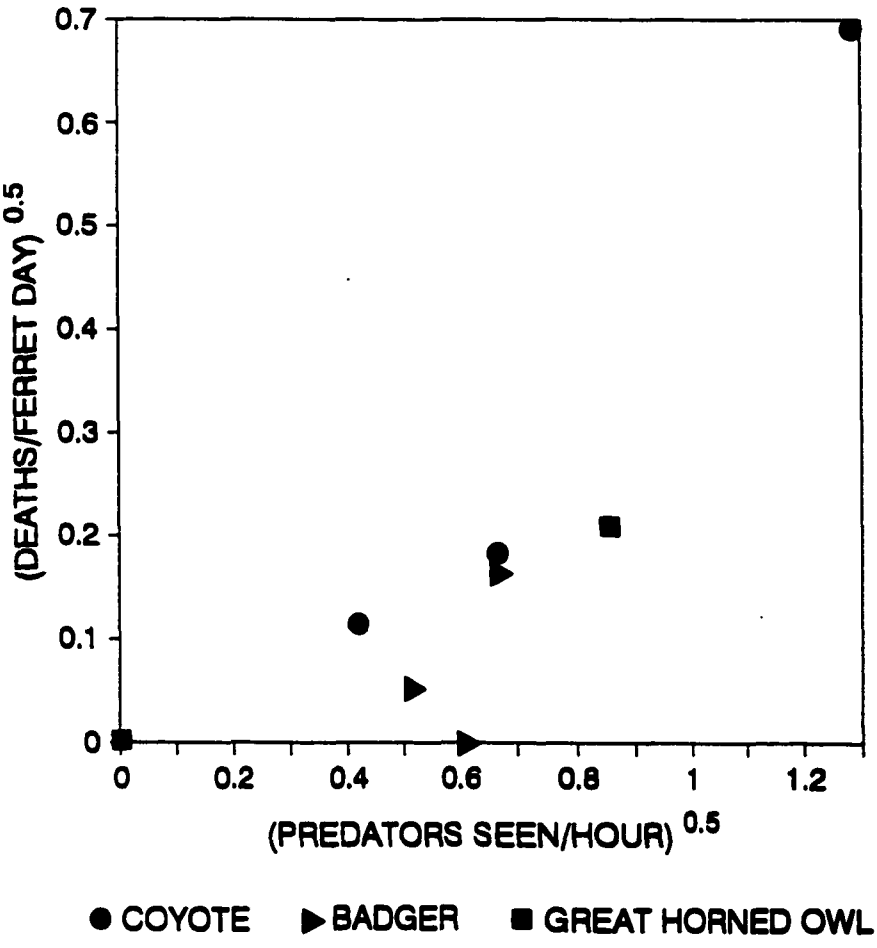

Figure 3.1. Relationship between numbers of predators seen on survey routes and predator-specific mortality rates for released Siberian polecats and black-footed ferrets. Measures are square roots of rates (on both axes).

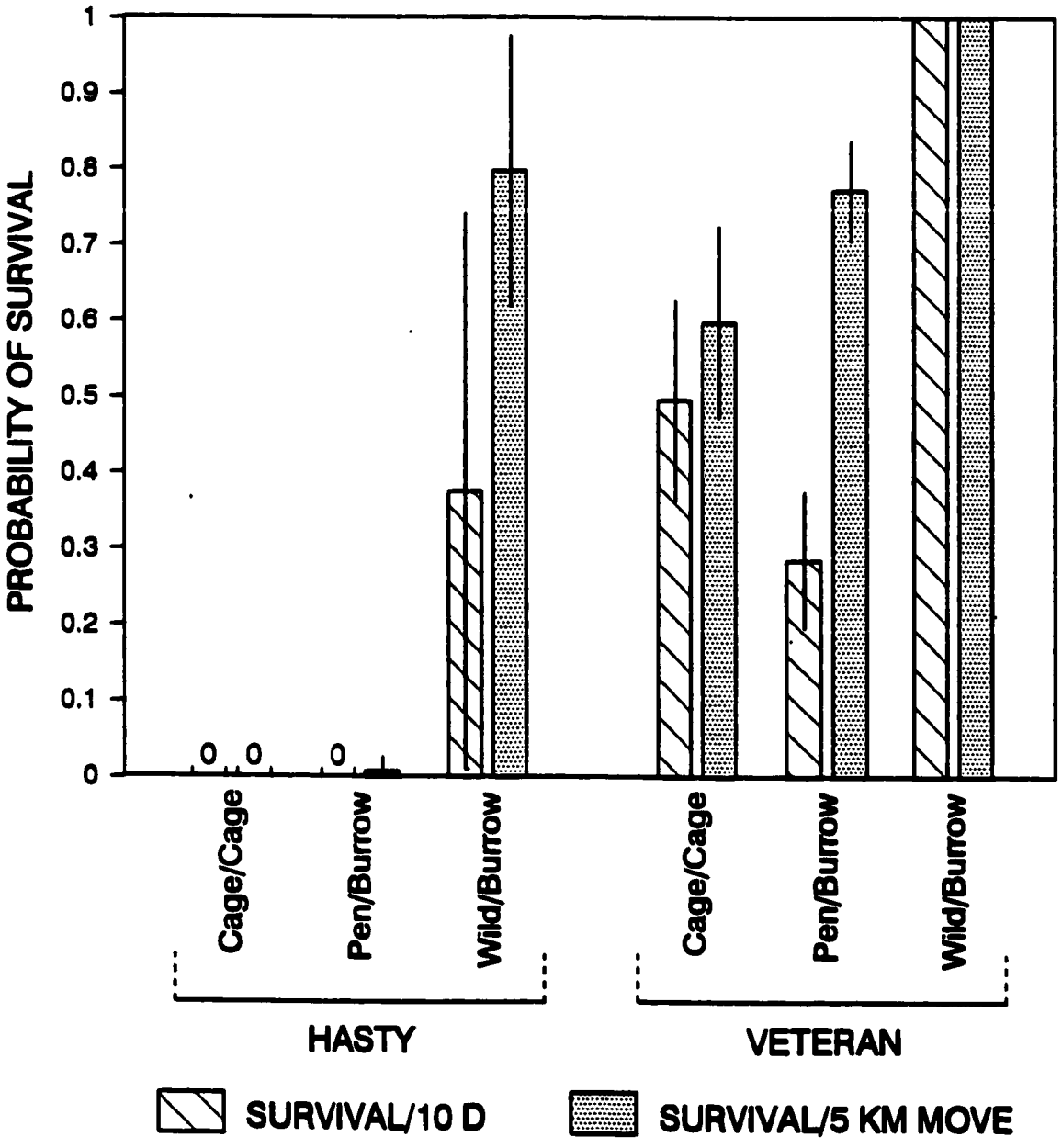

Figure 3.2. Time-based and movement-based probabilities of avoiding predation for Siberian polecats with 3 rearing histories and 2 release methods (rearing/release). Bars indicate means ± 1 standard deviation.

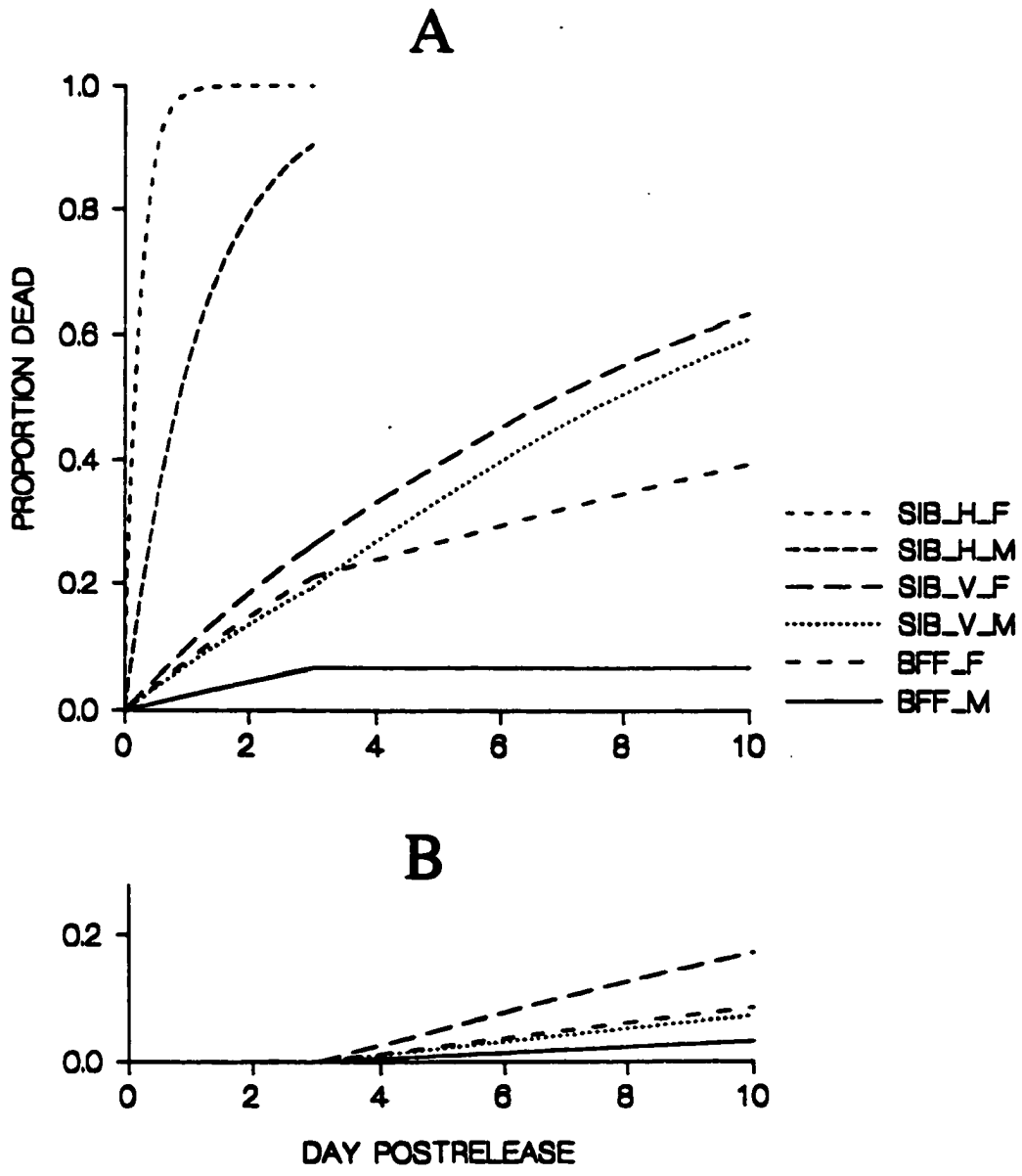

Figure 3.3. Models of (A) predation and (B) starvation for captive-reared black-footed ferrets and Siberian polecats spanning ten d postrelease. (SIB=Siberian polecat; BFF=black-footed ferret; F=female; M=male; H=Hasty, Colorado; V=Veteran, Wyoming).

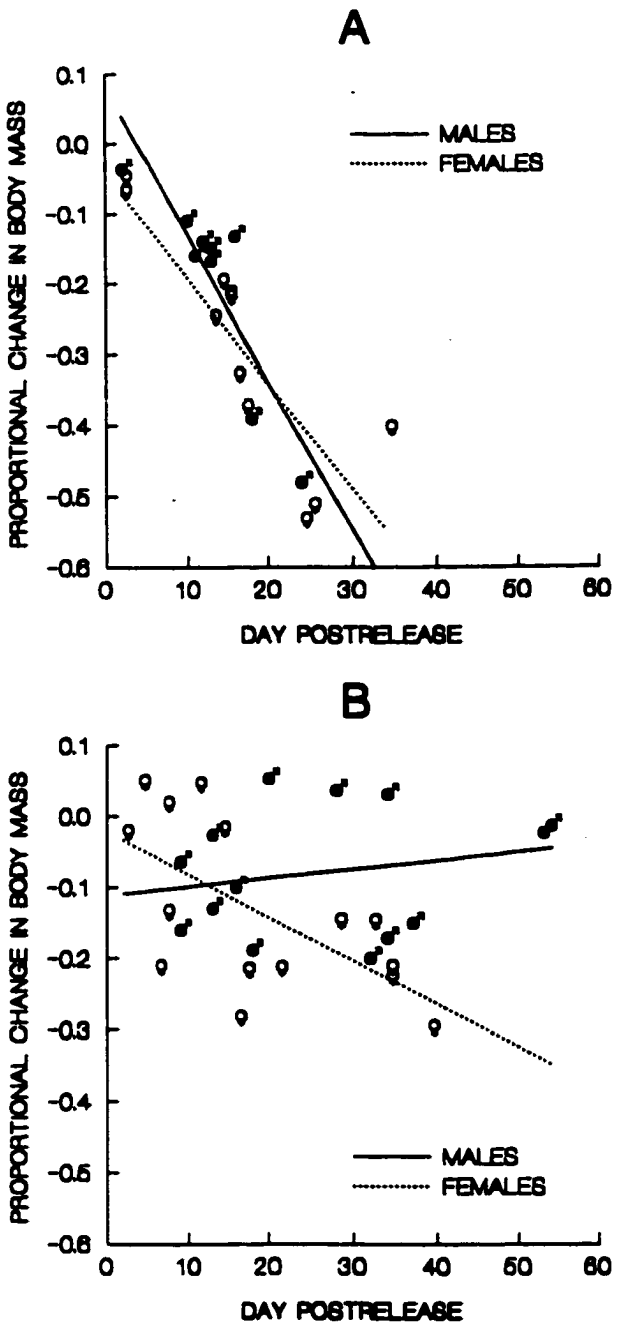

Figure 3.4. Change in body mass of (A) Siberian polecats and (B) black-footed ferrets after release onto prairie dog colonies (change expressed as a proportion of prerelease mass).

CHAPTER 4

TEMPORAL AVOIDANCE OF PREDATORS BY SIBERIAN POLECATS AND BLACK-FOOTED FERRETS[1]

ABSTRACT

Siberian polecats (Mustela eversmannii) and black-footed ferrets (M. nigripes) can hybridize and have been labeled as ecological equivalents. These polecats and the hybrids have been used as investigational surrogates for black-footed ferrets in several types of studies, the interpretation of which is clouded by incomplete understanding of the differences between the 2 mustelids. Further awareness of comparative behaviors may benefit discussions regarding genetic manipulation to assist the inbred black-footed ferret population. We contrasted behaviors of free-ranging radio-tagged polecats and ferrets released onto ferret habitat. Ferrets avoided daylight, used crepuscular periods significantly less than time available, and preferentially used the post-midnight hours. Polecats tended to avoid day, but were not significantly selective for any period of the night. Ferrets and polecats moved most during brightly moonlit nights; spotlight searches for ferrets will be most efficient if conducted during moonlit periods, and dispersal of reintroduced ferrets may be reduced by releasing them during the dark phase of the moon.

---

[1]Formatted for submission to *Journal of Mammalogy*

The diel activity pattern of released ferrets was consistent with avoidance of coyotes (Canis latrans) and diurnal birds of prey, in contrast with the pattern of released polecats. Data extracted from published telemetric studies done in Qinghai, China, however, demonstrated a pattern of temporal avoidance of red foxes (Vulpes vulpes) by Siberian polecats in their natural habitat. Intraguild predation (including interference competition) is inferred as a selective force influencing behaviors of these mustelids, and may be responsible for restricting the niche of black-footed ferrets.

INTRODUCTION

Siberian (steppe) polecats (Mustela eversmannii) and black-footed ferrets (M. nigripes) have been termed "ecological equivalents" (Hoffmann and Pattie, 1968; Chap. 3), are capable of interbreeding and producing fertile offspring (Davison et al., 1999), and have been considered conspecific (Heptner et al., 1967). Because the steppes of Asia and North America are geographically separated, and are not identical, natural selection may have favored divergence between the 2 forms, and both the randomness of mutation and genetic drift could have promoted differing traits. Indeed, black-footed ferrets and Siberian polecats are distinguishable by hair length and coloration, but not by cranial morphology (Anderson et al., 1986). Genetic studies have been inconsistent regarding species level relationships (Davison et al., 1999; O'Brien et al., 1989; Villablanca, 1996).

Evaluation of the similarity of Siberian polecats and black-footed ferrets is important beyond phylogeny. Black-footed ferrets became nearly extinct in 1985, when epizootics of canine distemper and plague (Yersinia pestis) struck the last known population (Forrest et al., 1988; Williams et al., 1988) near Meeteetse, Wyoming (Fig.

4.1). The population was reduced to 10 animals during winter, 1985-86 (Miller et al., 1996), and all individuals, including wild-born progeny from 1986 were captured for a captive breeding program by 1987. Because of the rarity of black-footed ferrets, Siberian polecats repeatedly have been used as research surrogates (references in Chapters 1-3), and interpreting results requires an understanding of the biological similarities and differences between the 2 animals. Furthermore, the relative lack of genetic variation in the bottlenecked, inbred population of black-footed ferrets, and the fact that these ferrets and polecats can interbreed, suggests that infusion of Siberian polecat genes into the black-footed ferret population may be beneficial. An improved understanding of the similarities and differences between black-footed ferrets and Siberian polecats should assist decisions regarding genetic manipulations.

Differences between these mustelids may extend to their predator avoidance behaviors. Predation caused 6 of 9 known losses of black-footed ferrets reintroduced in 1991 (Chap. 3), emphasizing the potential importance of predator avoidance. Captive-reared Siberian polecats released onto black-footed ferret habitat suffered even higher rates of predation than did black-footed ferrets (Chap. 3). This difference may have been due to predator avoidance behaviors that differed from those of black-footed ferrets due to differences in natural selection in their respective ecosystems.

Antipredator defenses may include activity patterns that reduce encounters with dangerous predators; such behaviors may be partly heritable, and may involve active decision making (Lima and Dill, 1990). Nocturnality and preference for dimly-lit periods during night to reduce risk of predation is a common theme in rodents (Brown et al.,

1988; Clarke,1983; Kaufman and Kaufman, 1982; Kotler, 1984; Kotler et al., 1988; Kotler et al., 1991 Lockard and Owings, 1974a; Vickery and Bider, 1981;), but has also been reported for members of other mammalian orders such as Chiroptera (Fenton et al., 1977; Morrison 1978; Rydell et al., 1996), Lagomorpha (Fafarman and Whyte, 1978; Gilbert and Boutin, 1991; Kolb, 1992; Rogowitz, 1997; Smith, 1990;), Insectivora (Vickery and Bider, 1981), and Carnivora (Cresswell and Harris, 1988; Debrot et al., 1985; Joshi et al., 1995); predator avoidance is often cited as the likely evolutionary cause. This strategy also has costs, as illustrated by exceptions and modifications to the theme (Alkon and Saltz, 1988; Lechleitner, 1958; Lockard and Owings, 1974b; Price et al., 1984; Smith, 1990; Stewart and Bider, 1977; Villafuerte et al., 1993). The following generalizations seem to apply to members of mammal species preferring to be active during dimly lit periods: (1) all are common prey for several species of predators, (2) members of small species avoid bright moonlight more often than do members of large species, and (3) they are able to forage efficiently in relative darkness (many are herbivores, take "prey" otherwise incapable of evasive action, and rely primarily on senses other than vision during foraging). These characteristics apply to black-footed ferrets. The potentially devastating effect of predation on ferrets was underscored in recent experimental releases (Chap. 3; Biggins et al., 1999). Because ferrets hunt and kill prairie dogs (Cynomys spp.) mostly in the darkness of burrows, time of night and moonlight should be unimportant to them for hunting. Consequently, circadian patterns of ferrets can be set by other aspects of their life history, such as predation on them. We predicted,

therefore, that black-footed ferrets would avoid diel activity peaks of their predators, and to avoid predation themselves, would be most active when moonlight was dim.

Siberian polecats in Asia hunt during both day and night (Heptner et al., 1967; Zhou et al., 1994b), kill prey both aboveground and within burrows (Denisov, 1984), and are in turn killed by various predators (Kydyrbaev, 1988). Siberian polecats, therefore, may be presented with problems of optimization more complex than those of black-footed ferrets. Tradeoffs in foraging and predator avoidance may vary seasonally and across the species' range, which extends for 7500 km from eastern Europe nearly to the Pacific coast (Stroganov, 1962).

Using radio-telemetry data on polecats and ferrets released onto prairie dog colonies (Chap. 3), we compared their diel activity patterns, and examined the effect of moonlight on activity. We also compared activity patterns of polecats and ferrets to published data on activity cycles of their most common predators.

METHODS

Study sites and subjects.–We reproductively sterilized Siberian polecats > 3 weeks prior to release by removal of oviducts from females and the vasa deferentia and epididymides of males (Chap. 3). To minimize effects on behavior, we left ovaries and testes intact. We experimentally released polecats on black-tailed prairie dog (Cynomys ludovicianus) colonies near Veteran, Wyoming in 1989 and 1990, and near Hasty, Colorado in 1990 (Fig. 4.1). We reintroduced black-footed ferrets into white-tailed prairie dog (C. leucurus) colonies in Shirley Basin, Wyoming in 1991 (Fig. 4.1). We provided all ferrets with postrelease food and release cage refugia, and gave some polecats similar

support (Chap. 3). To limit our analyses to animals that behaved most naturally, we used only those data collected > 3 d after artificial support had ended. This restriction, plus mortality and collar loss (Chap. 3), eliminated all data for 44 of 55 polecats and 17 of 37 ferrets radio-monitored at the time of release.

Radiotelemetry.–We radio-tagged polecats and ferrets using 10 g transmitter packages with degradable wool collars and 20 cm whip antennas (Chap. 3). Pulse intervals of motion-sensitive transmitters (0.9-2.4 s) were inversely proportional to activity of the collared animals. Pulse intervals were controlled by circuitry that calculated a moving average of number of times a motion-sensitive mercury switch was actuated during the previous 10 s.

We radio-tracked primarily using triangulation from pairs of fixed stations fitted with 11-element, dual-beam Yagi antennas on 6.1 m masts, operated continuously during night (Biggins et al., 1999). Data points were estimates of location for each aboveground animal, separated by 15.58 ± 0.35 min. ($\bar{x}$ ± SE). Radiotracking during day was a mixture of triangulation and non-positional monitoring from single stations. Non-positional monitoring indicated changes in presence or absence of radio signal and pulse interval when a signal was present. Automated strip chart recording was used to monitor some animals whose transmitters were not simultaneously audible from at least 2 fixed stations.

We estimated the angular error of each fixed tracking station by repeatedly (50-90 times) calculating differences between a known azimuth to a test transmitter read from a surveyor's transit and an azimuth obtained using radio-telemetry (Biggins et al., 1999). We moved the test transmitter in an arc around the tracking station at a range of 500-1500

m, stopping at about 3 degree intervals. We used standard deviations of the differences to estimate an error arc (Biggins et al., 1999) for each station, and used intersecting error arcs to calculate areas of error quadrangles (EQ) (White and Garrot, 1990) that accompanied each location estimate for an animal. We used multiple beacon transmitters to reference stations.

Radio-tracking error is a nuisance variable that can confound interpretation of effects of primary treatments. Errors in simultaneous bearings taken on a moving animal can result in overestimation or underestimation of the actual move, but inconsistency in consecutive bearings taking on stationary animals causes artificial "movements" which result in overestimation of cumulative moves. Long cumulative movements may have taken animals long distances from stations causing poor angles of intersection or necessitating use of less accurate stations. Both of these phenomena result in a positive correlation between EQ and movement. Whether changes in error are the cause or consequence of movement determines the utility of including error as a covariate in statistical models. Because of the theoretical basis for artificial increase in movement due to error, because long movements were rare, and because we attempted to minimize telemetry error during long movements by careful selection of tracking stations, we chose to incorporate error into our statistical models. In addition, we examined separately the correlation between mean EQs per bout and cumulative movements for bouts, using all bouts for both species.

Animal activity.--A nested series of questions guided the strategy for data analysis, and different subsets of data were required to address each (Table 4.1). We first tested for

overall differences in activity rates between species. Second, we tested for differences in activity by time of day (diurnal, nocturnal, crepuscular), followed by a finer-grained test of differences during blocks of non-day times. Third, we tested for differences in activity depending on the presence of moon. Finally, when the moon was present, we tested for effects of amount of illumination on nocturnal activity.

We derived 2 indices of activity based on presence or absence of radio signal in combination with either (1) pulse interval (PI) of the motion-sensitive transmitters, or (2) simultaneous bearings from ≥ 2 stations giving estimates of location. We defined activity in bouts as 2 or more consecutive observations classified as active and separated by < 1 h. Some bouts were truncated by cessation of monitoring. A few "partial bouts" are assumed to be in the dataset; a bout cannot be proven to be complete unless an animal emerged ≥ 1 h after monitoring began and became inactive ≥ 1 h before monitoring ended. Measures used in analyses were cumulative distances traveled per bout (location-based bouts only) and numbers of bouts. We classified each bout according to moon condition and time category when the bout began, even if the bout continued into other categories. Statistical methods included preference analyses (availability vs. use), and multivariate general linear modeling.

In general, receiving a signal from an animal's transmitter at 2 or more stations indicated the animal was aboveground because stations were separated by 1-8 km. The deeper a transmitter was belowground, the closer the receiving antenna had to be to receive a signal. At 2 m belowground, a typical depth for a prairie dog burrow, signals could be received only a few meters from directly above the transmitter. Transmitters at

shallower depths could be heard sometimes from stations within 500 m, and transmitters of polecats in the shallow burrows of pocket gophers (Geomyidae), were audible from greater distances.

Animals at all 3 study sites were tracked consistently from 2 or more stations during night. Day monitoring for black-footed ferrets and some polecats consisted of listening from a single, strategically located station to detect audible signals and to time pulse intervals for motion-sensitive transmitters.

We used pulse interval (PI) based data for day/night comparisons because these data could be derived equally well from single or multiple station tracking strategies, increasing the quantity of data available during day. Bouts derived from location estimates were preferred for all other comparisons because they were unlikely to have been generated from belowground signals. Eliminating underground signals was important for comparisons between species.

Monitoring activity using estimates of location.–We defined location-based monitoring time for each animal as time spent radio-tracking from multiple stations to estimate locations of that animal when it was aboveground. It included time when the subject was not located because it was belowground, but did not include time when the subject was not within signal-receiving range from at least 2 stations. Location-based bouts began when an animal was first located and continued as long as subsequent locations were separated by < 1 h, or until the monitoring session ended. Estimates of moves and their elapsed times based on consecutive relocations also were assigned lunar and time categories present during the first location defining the move, but without respect

to classification of bouts (which was based on conditions at the beginning of each bout). For these estimates, we split movements and times that spanned > 1 category. The 2 categories each accumulated a portion of the elapsed time between relocations determined by the time of change in category, and distance was segregated in proportion to the split in time.

Monitoring activity using pulse interval.–Bouts of activity defined by clustered consecutive instances of signal presence (using the maximum of 1 h separation) from a single station could include belowground signals from animals that were inactive. Classifying activity based on pulse interval made certain that an animal was active (but not necessarily that it was aboveground). We accumulated PI-based monitoring time for an animal whenever an animal's transmitter could produce a signal (if it were aboveground) of sufficient quality for receiving equipment to time pulses from at least 1 station. PI-based bouts began when an observation had a PI < 2.0 s and ended when an observation of PI ≥ 2.0 s, when an inter-observation span exceeded 1 h, or when monitoring ended.

Diel periods and lunar measures.–We obtained times of sunrise, sunset, moonrise, and moonset, and moon illumination values, from the U.S. Naval observatory data (1999) for Lamar, Colorado (25 km east of the Hasty site), Torrington, Wyoming (22 km northeast of the Veteran site), and Medicine Bow, Wyoming (25 km south of the Shirley Basin site). The calendar day was divided into 7 categories (Table 4.2), which were recombined into 2-5 categories depending on the type of analysis.

Use and availability.--A common problem arising in selection studies employing radio-telemetry is non-independence of consecutive data points (Aebishcer at al., 1993;

Swihart and Slade, 1985; Thomas and Taylor, 1990;). Individual estimates of location in our study were serially correlated, with only minutes between them, but series of such estimates were summarized in bouts. Bout summaries (in contrast to summaries by animal) gave greatest weight to the most successful animals; longer survival times enabled increased sample sizes of bouts monitored. To evaluate further the assumption of independence of bouts, we used the Durbin-Watson test for first-order autocorrelation (Neter et al., 1996). Also, we examined serial correlation plots of residuals in multivariate general linear models with multiple animals, and for simpler models for each of the 5 individual animals with largest sample sizes (17-48 bouts).

Definitions of availability can have profound effects on conclusions regarding selection and avoidance, and some definitions have been somewhat arbitrary (Aebischer et al., 1993; Johnson, 1980; McClean et al., 1998). We monitored individual animals for varying lengths of time due to release sequence, mortality, dispersal, and loss of radio-collars. We defined availability, however, as monitoring within time categories and animals, and measured it without variation. This design allowed us to apply the selectivity analysis of Neu et al. (1974), involving a Chi-square test for goodness of fit to evaluate overall differences in proportionate use (numbers of bouts) and availability (proportion of monitoring time) between 2 or more categories. Although sample sizes met minimum criteria for the traditional Chi-square test (Alldredge and Ratti, 1986, 1992), we used the less restrictive exact Chi-square procedure (Berry and Mielke, 1985) for overall tests. These omnibus tests, if significant, were followed by calculation of Bonferroni-adjusted

confidence intervals based on the z-statistic to evaluate selection and avoidance in individual categories (Neu et al., 1974).

PI-based data facilitated comparisons of bouts counts between day and non-day categories (Table 4.2). During non-day (categories 1-6, Table 4.2), we consistently monitored movements by telemetric locations, and used location-based bouts to characterize activity. For evaluation of diel patterns, we combined periods 1 and 2 (Table 4.2) into a "crepuscular" category for the evening, and combined periods 5 and 6 into a morning "crepuscular" category. To assess overall correspondence between activity and monitoring time (availability) for the 4 non-day categories, we used the omnibus Chi-square test, followed by calculation of Bonferroni-adjusted confidence intervals to assess the selection/avoidance of individual categories.

We used a combination of periods 2 + 3 + 4 + 5 ("night," Fig. 4.2) to assess moon effect, assuming the sun had no influence from 1 h after sunset until 1 h before sunrise. Each bout was tagged with a moon influence value which was the proportion of the moon illuminated by the sun, or "0" if the moon (1) was overwhelmed by sun's influence, (2) had not yet risen or already set, or (3) was in the "new moon" phase. The moon influence value was > 0 if the moon provided primary illumination and was present at any time during the bout. Because we did not directly measure illumination at night, moon illumination values indicate potential brightness. Atmospheric conditions such as clouds, and ground conditions such as snow cover and type of vegetation, affect light levels. Cloud cover, in particular, will reduce illumination, causing overestimation of both availability and use of the "bright" categories. The effect of this bias is expected to depend

on the actual preferences of the animals for brightness and the amount of misclassification. We did not maintain data on cloud cover, but the region where our studies took place is relatively arid. Regional averages for eastern Wyoming and Colorado indicate about 30 % of the days in October have at least partial cloud cover, but only 18 % of the days in October have measurable precipitation (≥0.25 mm). Because those days with precipitation are not often full days, these general weather data support our perception that few moonlit bouts of ferret or polecat activity were likely to have been effected by cloud cover thick enough to dramatically reduce the level of light.

For evaluating the effect of moon presence on ferret and polecat activity, we grouped nights based on moon presence, moonrise, and moonset (Fig. 4.2). "Dark" nights were those with < 1.5 h of moonlight available, "moonlit" nights had < 1.5 h without moonlight, and "mixed" nights were the remainder. Because moon phase and moonrise cycles are monthly and synchronous (Fig. 4.2), dark nights are associated with low moon illumination, moonlit nights with nearly full illumination, and mixed nights with partial illumination.

We used the Neu et al. (1974) method to examine preference for moonlight. First, we compared numbers of bouts and availability for moonlit nights and dark nights. In a second comparison, we compared numbers of bouts and availability during moonlit and dark periods within the "mixed" night category.

To examine further the effect of brightness when the moon was present, we assessed distances moved/bout during nights when moon illumination was ≥ 20 % (including all of the moonlit nights and part of the mixed nights), again using multi-variate

general linear modeling. If the moon was present during any portion of a bout, we assigned its illumination value to the entire bout.

We produced an overall summary of combined effect of moon and nightly periods on activity of ferrets and polecats by summing all movements within 4 temporal categories. We redefined these categories so that 2 of them ("NIGHT-PM" and "NIGHT-AM") covered all time lacking effect of sun (sunset + 1 h to sunrise - 1 h), then split each of these 2 categories into subcategories of moon present and moon absent. The additional 2 crepuscular periods (1 and 6, Table 4.2) encompassed the remainder of time from sunset - 0.5 h to sunrise + 0.5 h (i.e., these "SUNRISE" and "SUNSET" periods were 1.5 h each). We summarized cumulative movements relative to cumulative monitoring times in these categories.

Rearing backgrounds and sexes of animals.--Although rearing history and sex can be important factors influencing survival of ferrets and polecats (Chapters 3,5; Biggins et al., 1999), we assumed that the restriction of this study to relatively successful animals tended to remove individuals with maladaptive traits, regardless of their backgrounds. The disproportionate mortality of cage-reared polecats (Chap. 3), for example, resulted in their poor representation (n = 3) in this subset, compared to wild-born or pen-experienced polecats (n = 8). Further subdivision of these 11 polecats into rearing groups, combined with other categorical predictors, would have resulted in models with more parameters than justified by the sample size (empty cells would have been 1 result). All black-footed ferrets in this study were cage-reared. Rearing and sex, therefore, were not incorporated into these evaluations.

Black-footed ferret and coyote activity patterns.--To compare the nightly activity patterns of coyotes (Canis latrans) with those of released black-footed ferrets and Siberian polecats, we extracted data from published studies of coyotes in Nebraska (Andelt and Gipson, 1979), Colorado (Gese et al., 1989), and Idaho (Laundré and Keller, 1981; Woodruff and Keller, 1982). The Colorado study area was within the historic range of black-footed ferrets and in an area with prairie dogs, and the Nebraska study area was at the edge of the historic range of black-tailed prairie dogs (Fig. 4.1). The Idaho study areas had habitat (shrub-steppe) similar to those of our study sites and were relatively close to the range of prairie dogs (Fig. 4.1). Original coyote data were presented in figures, necessitating extrapolation of hourly or half-hourly observations of movements, from which we calculated averages for each of the 4 non-day categories described above. We then converted mean movements to proportions of nightly moves in each time category for each study and species to allow direct comparison. The estimate for each time category for coyotes was the mean of the 4 studies. If several seasons were presented, the season most closely approximating the fall period of our study was used.

The Idaho studies allowed relatively accurate classification of data relative to sunrise and sunset (a prerequisite for our categories), but the Laundré and Keller (1981) study was conducted in July and August, and the Woodruff and Keller (1982) study had categorical measures of movements, necessitating estimation of midpoints. For the Nebraska study, sunrises and sunsets during the lengthy season used (16 November-28 February) varied by 50 min and 78 min respectively; midpoints of sunrise and sunset were provided, but incorrect classification of some data was inevitable, which could be

especially influential in the 2.5 h twilight categories. A similar problem in the August-November Colorado data was exacerbated by inclusion of the autumnal equinox, when the rate of change in day length was greatest, resulting in a 109 min change in sunrise and a 142 min change in sunset during their study. Black-footed ferret and polecat data used in this comparison were total distances moved in each of the 4 non-day categories, adjusted by monitoring time in those categories.

Siberian polecat and red fox activity patterns.--Red foxes were the most important natural predator of Siberian polecats during a study on the Tibetan Plateau in Qinghai Province, China (Zhou et al., 1994a). Data on summer activity patterns of polecats and foxes were available from telemetric studies conducted at that site (Zhou et al., 1994b; Zhou et al., 1995). We extracted information directly from figures in those reports to compare the 2 species.

RESULTS

Data overview.–Using telemetry we monitored Siberian polecats for a total of 1371 h and black-footed ferrets for 5245 h. Polecats and ferrets moved a total of 111.7 km in 89 bouts and 122.7 km in 201 bouts respectively (Table 4.3), resulting in mean cumulative movements of 1255 m/bout and 611 m/bout respectively. Polecats and ferrets moved > 2 km in 18 % and 5 % of bouts respectively. After engaging in numerous moderate bouts of activity during her first 9 d postrelease, 1 wild-born female polecat made no aboveground moves for 12 consecutive days, the longest continuous period belowground we documented for a ferret or polecat. She then abandoned the prairie dog colony, and moved to an area with yellow-faced pocket gophers (Cratogeomys

castanops), later making the 2 longest cumulative aboveground movements recorded for this study (10.4 and 11.2 km).

Telemetry error.--In an overall assessment of telemetry error using all movement based bouts, the relationship between area of error quadrangle (EQ) and estimated movement was site-specific (interaction; $F = 6.843$; d.f. = 1, 280; $P = 0.009$), probably due to arrangements of tracking stations. The correlations between EQ and movement were significant in separate analyses of polecats ($F = 5.641$; d.f. = 1, 83; $P = 0.020$) and marginally so for ferrets ($F = 2.966$; d.f. =1, 199; $P = 0.087$), but only 1-6 % of variation was "explained" by this variable. Log transformation of cumulative moves largely corrected the heteroscedastic and non-normal distribution of residual variation from the regression using non-transformed data, and was adopted for this and other analyses of movements. Because EQ effect was significant in this evaluation, it was forced into all future linear models involving movements to control for effect of telemetry error (regardless of its statistical significance in those models).

Independence of bouts.--We concluded that bouts could be considered as statistically independent observations because serial correlations of residual variation, which should be most evident in analyses of individual animals, were not significant (Durbin-Watson test, $R^2 < 0.03$, $P > 0.05$) in regression models with error quadrangle and moon illumination as predictors and cumulative movement/bout as the response. Plots of higher order autocorrelations also lacked predictable patterns. In final multivariate models with all animals, autocorrelation was small ($R^2 < 0.001$).

Species.–The overall, EQ-adjusted, rate of movement (mean ± standard error) for black-footed ferrets (544.6 ± 96.7 m/h) was significantly less than the rate of movement for Siberian polecats (1016.5 ± 119.8 m/h) ($F = 8.916$, d.f. = 1,22, $P = 0.007$), based on estimates for each animal derived from total cumulative distances and elapsed times between its consecutive relocations (separated by < 1 h). EQ was a noteworthy control variable in this statistical model ($F = 6.500$, d.f. = 1,22, $P = 0.018$). Without EQ, the unadjusted mean movement rates were 596.8 ±105.2 m/h for ferrets and 938.0 ± 128.9 m/h for polecats ($F = 4.203$, d.f. = 1,23, $P = 0.052$).

Day and night.--Black-footed ferrets engaged in far fewer pulse interval based bouts than expected (based on monitor time) during the day, compared to night (Fig. 4.3) ($X^2 = 222.647$, d.f. = 1, $P < 0.001$), in contrast to Siberian polecats, which seemed less selective ($X^2 = 3.277$, d.f. = 1, $P = 0.082$). Ferrets and polecats both were active aboveground 7.5 % of the time they were monitored during non-day periods, but, comparing distribution of bouts between periods, polecats were more crepuscular and ferrets were more nocturnal (Fig. 4.4) ($X^2 = 16.239$, d.f. = 1, $P < 0.001$). The difference could not be explained by availability because twilight monitoring was 36.7 % of total monitoring time for ferrets and 31.2 % of total monitoring for polecats. There was an overall difference in selection patterns for the 4 nightly categories for black-footed ferrets ($X^2 = 45.493$, d.f. = 3, $P < 0.001$), with the Bonferroni-adjusted confidence intervals suggesting significant selection ($P < 0.05$) for the early morning category and avoidance of the 2 crepuscular categories. The use of the 4 nightly categories by Siberian polecats did

not differ significantly from proportions based on monitoring time available in each cateogry (X^2 = 5.660, d.f. = 3, P = 0.128) (Fig. 4.4).

Moon.--During mixed nights, Siberian polecats made significantly more bouts of movement than expected (relative to monitor time) when the moon was present (Fig. 4.5) (X^2 = 8.157, d.f. = 1, P = 0.005) than when the moon was absent; a similar trend was not significant for black-footed ferrets (X^2 = 2.087, d f. = 1, P = 0.159). Ferrets tended to engage in more bouts than expected during moonlit than dark nights (X^2 = 3.913, d.f. = 1, P = 0.057), but the similar pattern for polecats was not significant (X^2 = 1.790, d.f. = 1, P = 0.262) (Fig. 4.5).

In the multivariate model of distances moved during bouts (treating moon illumination ≥ 20 % as a continuous variable), there were significant effects of species (F = 18.546; d.f. = 1, 131; P < 0.001), moon illumination (F = 31.240; d.f. =1, 131; P < 0.001), and a species by moon illumination interaction (F = 25.823; d.f. = 1, 131; P < 0.001). Because of the interaction, separate models were evaluated for each species. Siberian polecats significantly increased their movements with increasing moon illumination (F = 33.281; d.f. =1, 36; P < 0.001), but black-footed ferrets did not (F = 0.207; d.f. = 1, 96; P = 0.650).

In general, both species were most active during moonlight (Fig. 4.6), but the patterns differed by species and time of night. Unlike ferrets, polecats tended to move less during dark periods of the night than during crepuscular periods when the sun's effect remained, but night moves exceeded crepuscular moves when the moon was present. Ferrets were more consistently nocturnal than were polecats.

Black-footed ferret and coyote activity patterns.--Considering only non-day categories, evening twilight (sunset - 0.5 h to sunset + 2.0 h) was the time of greatest coyote movement and least black-footed ferret movement (Fig. 4.7), while post-midnight hours ("NIGHT-AM") had the least coyote and most ferret movement. Notwithstanding the shortcomings of adapting the coyote data and the lack of rigorous statistical treatment in this comparison, the negative correlation is suggestive of predator avoidance behavior by black-footed ferrets. Siberian polecats demonstrated no such tendency (Fig. 4.7).

Siberian polecat and red fox activity patterns.--Predator avoidance was also a plausible explanation for the summer activity pattern of polecats observed in Qinghai (Zhou et al., 1994b). Before sunset, activity of polecats diminished as activity of foxes increased. The time of highest nocturnal polecat activity (02:00) likewise corresponded to the time of lowest nocturnal fox activity, although foxes were quite active during all periods of night (Fig. 4.8). By sunrise + 2 h, polecat activity ceased, but foxes remained somewhat active until noon. Polecats resumed moderate activity in early afternoon, when foxes were inactive.

DISCUSSION

Moonlight.–We predicted the ferrets and polecats would avoid moonlight. Instead, polecats were more active during full moonlight. Preference for moonlight by black-footed ferrets appeared to be weaker than that of Siberian polecats. Because black-footed ferrets hunt prairie dogs in their burrows, and mostly at night, they seem to gain no advantage from high levels of ambient light for hunting. Ferrets may use moonlight, however, to navigate long distances for large-scale spatial learning of their home ranges, to locate

concentrations of prey, potential mates, and competing ferrets, or to detect predators. Coyotes are primarily visual hunters, but also frequently use scent and sound cues (Wells and Lehner, 1978). The scent glands of Mustela may enhance their detectability by canids, which may reduce the value of darkness for avoiding predation.

Perhaps we should not expect consistent avoidance of either full or new moon phases by ferrets or polecats because their metabolisms would not allow them to remain inactive for the duration of the moon's dark phase unless extra prey could be cached. A captive polecat starved to death in 5 d without food (Sviridenko, 1935). Caching is implied in cases where black-footed ferrets remained belowground for > 5 d (Biggins et al., 1986; Richardson et al., 1987), and for the polecat in this study that remained belowground for 12 d. Polecat-occupied burrows in Asia have been found to contain as many as 6 intact fresh suslik (Spermophilus spp.) kills (Sviridenko, 1935).

Intraguild predation and diel patterns of activity.–Intraguild predation (IGP), as defined by Polis et al. (1989), benefits the larger predator both from nutrition and from reduced competition. The common failure of coyotes to eat polecats and ferrets, and other small carnivores such as San Joaquin kit foxes (Cypher and Spencer, 1998), suggests reducing competition is more important than obtaining these animals as food. This IGP is asymmetric, because coyotes are always the predator on Mustela. A requisite for stable coexistence of 2 predators involved in asymmetric IGP is that the victim be a better exploitative competitor (Holt and Polis, 1997; Polis et al., 1989). Black-footed ferrets, with their ability to hunt prairie dogs when they are active aboveground or inactive

belowground, appears more effective at exploiting prairie dogs than are coyotes, although evidence is only anecdotal.

Temporal avoidance of predators in the IGP context is well-documented in aquatic systems (Gliwicz, 1986; references in Polis et al., 1989), and often leads to reduced resource acquisition by intraguild "prey" (Clark and Levy, 1988; Holomuzki, 1986; Stangel and Semlitsch, 1987). Black-footed ferrets, unlike the many organisms involved in predation-starvation tradeoffs (Lima, 1988; Lima and Dill, 1990; Sih, 1987), can avoid predators without notably compromising their foraging efficiency. Temporal avoidance of mid-sized predators should be critically important to small predators residing in the midst of a large biomass of attractive prey. A prairie dog colony in South Dakota was reported to have 5.7 times more coyotes and badgers (Taxidea taxus) than off-colony areas (Krueger, 1986).

The black-footed ferrets we studied were highly nocturnal, consistent with other studies (Biggins et al., 1986; Hillman, 1968). By avoiding the activity periods of their diurnal prey, black-footed ferrets decrease their probability of encountering other predators that hunt those prey. During daylight, diurnal raptors such as ferruginous hawks (Buteo regalis) and golden eagles (Aquila chrysaetos) hunt prairie dogs, and are a threat to ferrets (Biggins et al., 1999). The hazard of predation during daylight may have induced a niche shift to nocturnality in black-footed ferrets. Such a restriction in niche (Hutchinson, 1957) due to predation is similar to suggested causes for the temporal separation among sea birds (Harris, 1974; Watanuki, 1986) and between owls and hawks (Carothers and Jaksić, 1984; Jaksić, 1982).

The Siberian polecats we studied were not significantly nocturnal. In northwest China, polecats are mainly nocturnal in winter and spring, but day activity is common in summer and fall (Zhou et al., 1994b). Our study took place in the fall. Hybrid polecats (M. eversmanii X M. putorius) released in the Altai region of Russia in summer had crepuscular peaks of activity (especially morning), and were least active at night (Denisov, 1984). Others report Siberian polecats are nocturnal (Brom, 1954; Serrebrennikov, 1929), largely diurnal (Sviridenko, 1935), and demonstrate little selectivity for day or night (Heptner et al., 1967; Stroganov, 1962). The apparent contradictions may be due to regional and seasonal differences in behavior of polecats, or due to differences in methods used by researchers in different studies.

One polecat was killed by a diurnal raptor in our study (Chap. 3). Evidence of predation on Siberian polecats was found at about 20 % of the nests of 4 sympatric eagles (Aquila chrysaetos, A. heliaca, A. rapax, and Haliaeetus albicilla) studied in northern Kazakstan (Todd Katzner, pers. comm.), implying costs of diurnal activity for polecats during summer in Asia. Aboveground hunting of diurnal prey may be necessary for Siberian polecats in some seasons and habitats, however, wherein elevated risk of predation is presumably exchanged for reduced risk of starvation. Male polecats may not be able to enter burrows of their common suslik (Spermophilus spp.) prey, and some species of known prey (e.g., microtine rodents) have burrows too small for any polecat. Under these circumstances, activity of Siberian polecats may become synchronized with activity of their prey, as shown for European polecats (Lode 1995).

The preference of black-footed ferrets for activity in the post-midnight hours and their significant avoidance of evening and morning crepuscular periods may be a canalized behavior due to selective pressure by coyotes. This activity pattern was evident in the wild Meeteetse population of ferrets (Fig. 1 in Biggins et al., 1986), and persisted through several generations of captive-bred ferrets (Fig. 2 in Vargas and Anderson, 1998). The captive-reared ferrets, maintained in cages and fed during the day, should have abandoned the post-midnight peak of activity, if that behavior were due to risk assessment and choice (Lima and Dill, 1990). A consequence of being active at the wrong times may be illustrated by the high predation rates on Siberian polecats of our study (Chap. 3). The activity patterns of polecats and coyotes were more closely matched than those of ferrets and coyotes, and more polecats than ferrets were killed by coyotes (26/55 vs. 5/37 respectively). Densities of coyotes, however, were higher at the polecat release sites than at the ferret release site (Chap. 3), providing an equally plausible explanation for variation in mortality rates. In their native habitats in China, activity patterns of Siberian polecats and red foxes were negatively correlated (Zhou et al., 1994b, 1995). The evidence suggesting polecat avoidance of foxes, however, is weaker than the ferret/coyote link, and there are insufficient data on free-ranging polecats to assess the role of canalization, risk assessment, or decision-making.

The victim of IGP should avoid the activity periods of the prey of its antagonist (whether the food habits of the 2 predators are, or are not, identical). For ferrets, this may involve avoiding the main activity periods of leporids, because leporids are a large part of the coyote diet in steppe and shrub-steppe ecosystems (Clark, 1972; Ellis and Schemnitz,

1958; Fichter et al., 1955; Gier, 1968; Johnson and Hansen, 1979; MacCracken and Hansen, 1987; Meinzer et al., 1975). North American Leporids have crepuscular peaks of activity (Lepitzki, 1990; Lord, 1964; Mech et al., 1966; Rogowitz, 1997; Smith, 1990), providing an explanation for preference of crepuscular hours by coyotes.

Ease of hunting or killing does not seem to be an adequate explanation for the activity pattern of ferrets. Sleeping prairie dogs are probably not found or killed more easily by ferrets. Burrows may help ferrets and polecats kill large prey (Vargas, 1994), and these animals chase prey into burrows, where kills are made (Clark et al., 1986; Denisov, 1984; Hillman, 1968; Paunovich and Forrest, 1987). This tactic seems equally adaptable to day or night. During a study of ontogeny of predatory skills, ferrets awakened sleeping prairie dogs before administering a killing bite to the throat (Vargas, 1994).

Intraguild predation and black-footed ferret populations.--If selective pressure from coyotes has influenced evolution of behavioral patterns in black-footed ferrets, effects of asymmetric IGP (Polis et al., 1989) on ferret populations would not be surprising. Removal of coyotes resulted in increases in badgers, bobcats (Felis rufus) and gray foxes (Urocyon cineroargenteus) in a Texas study (Henke and Bryant, 1999), although the changes may have been from combined influences of IGP and less direct interactions in the faunal community. Factors that favor coyote populations may be detrimental to ferret populations. One such factor may be the density and distribution of leporid prey. Densities of cottontails (Sylvilagus audubonii) were up to 27 times greater on black-tailed prairie dog colonies in Colorado than on grasslands without prairie dogs (Dano, 1952; Hanson and Gold, 1977). The largely synchronous cycling of populations of

coyotes and leporids in some areas (Clark, 1972; Cypher and Spencer, 1998; Maccracken and Hansen, 1987; O'Donoghue et al., 1997) underscores the importance of leporids as prey of coyotes, and may promote a similarly cyclical hazard rate for predation on ferrets. In addition to this numerical response, a behavioral response by coyotes to reduced leporid numbers may benefit ferrets; coyotes may increase their hunting of prairie dogs, further decreasing the hazard rate for ferrets as remaining coyotes become less nocturnal. Declines in leporids seemed to precipitate similar switching to sciurid prey by lynx (Lynx canadensis) and to murid prey by coyotes in Canada (O'Donoghue et al. 1998), but may have intensified intraguild predation by lynx on red foxes in Alaska (Stephenson et al. 1991).

Other factors that depress coyote populations could decrease mortality rates for ferrets. Coyote control is an example which has been practiced on most ferret release areas (Chap. 3, 5; Biggins et al., 1998). Wolves (Canis lupus), once common on the Great Plains (Fig. 4.1), may have historically influenced coyote distribution and populations. Range expansion of coyotes seems correlated with wolf extirpation (Nowak, 1978), and the ranges of wolves and coyotes do not overlap in Minnesota (Berg and Chesness, 1978) and part of northeastern Alberta (Fuller and Keith, 1981). Instances of coexistence seem mediated by proximity to man and his alterations of habitat (Thurber et al., 1992), or by a scavenging tactic adopted by some coyotes that takes advantage of the wolf pack's ability to kill large prey such as moose (Alces alces), elk (Cervus canadensis) and bison (Bison bison), that cannot be rapidly consumed (Paquet, 1991, 1992). Even in examples of coexistence, however, coyotes were killed (but often not eaten) by wolves. Thus,

"mesopredator release" (Soulé et al., 1988) can be added to the list of factors (e.g., rodent control, cropland conversions, plague, canine distemper) that may have contributed to the decline of black-footed ferrets. North American wolves, however, may have killed ferrets, similar to predation on Siberian polecats by Asian wolves (Heptner and Naumov, 1967; Kydyrbaev, 1988), which could negate the value of reduced coyote populations. Secondary influences of predators involved in IGP have been implied in many field studies (see review of Polis et al., 1989), and demonstrated experimentally (e.g., Spiller and Schoener, 1990). Nevertheless, "a basic, humbling message emerging from the theoretical studies of complex webs is that with many potential routes for indirect interactions between any species pair, it may be difficult to predict the effect of 1 species upon another" (Holt and Lawton, 1994, p. 509).

Individual fitness, other considerations.--Predation avoidance has been emphasized in this paper because it is a critical issue. Foraging and energetics were not central themes here, but must be considered in attempts to explain the behavioral differences between Siberian polecats and black-footed ferrets. If polecats spend more time than black-footed ferrets hunting aboveground, benefits (prey acquired) must outweigh costs (energy expended and risk of predation). For both species, cost/benefit ratios may change seasonally and differently for males and females. Males, for example, may increase individual fitness by becoming more risk-prone when it is important that they contact as many females as possible. Likewise, it may become profitable for a female to engage in riskier hunting tactics during the energetically demanding period of caring for a litter.

Night temperatures in winter may produce a substantial thermoregulatory cost for aboveground activity by black-footed ferrets. Ferrets, however, seemed more nocturnal in winter than in summer (Biggins et al., 1986), similar to Siberian polecats (Zhou et al., 1994b,). Because ferrets do not tunnel under the snow (Richardson et al., 1987), they are conspicuous when moving on snowy terrain. With snow cover, visually-hunting diurnal predators may become disproportionately more effective than nocturnal predators, increasing the cost for daytime activity by ferrets. To reduce risk of predation, American martens (Martes americana) in some climates may increase thermoregulatory costs by being active at night during winter (Drew and Bissonette, 1997). Alternatively, increased hunting efficiency may require hunting at night (Zielinski et al., 1983), and heat produced by activity may be used for thermoregulation during cold nights (Sandell, 1989).

Seasonal changes in pelage seemed more pronounced in our captive polecats than in captive ferrets, with winter hair of polecats becoming longer and lighter-colored. If polecats are better insulated than ferrets in winter (a topic that needs further investigation), the adaptive value may be related to their tendency to be more active aboveground than are ferrets. Polecats in our study moved at about twice the rate of ferrets. Maximum distances moved/d by Asian polecats observed by snow-tracking (15 km/d; Kydyrbaev, 1988; Zverev, 1931), and by following animals (19 km/d; Denisov, 1984), again were about double the maximum move/bout for wild black-footed ferrets at Meeteetse (7 km).

Telemetry error.--Assuming that telemetry error caused some "movement," use of EQ as a covariate in models to assess movement increased the apparent power of some

tests by accounting for a portion of the "noise," and in other cases may have protected against unwarranted rejection of hypotheses. Although careful study design can distribute telemetry error relatively equally among treatment groups, we suggest error estimates should be used as covariates in analyses of spatial data whenever telemetry error is suspected of producing spurious movements, even at low frequency or magnitude. Such use is uncommon, and was not listed by Saltz and Alkon (1985) in their assessment of the 4 principal applications of error estimation in radio-tracking studies.

Management implications.–Although Siberian polecats and black-footed ferrets are similar in many respects (Clark et al., 1986; Miller and Anderson, 1990, 1993), behavioral differences were detected in our study. Movements of our captive-bred black-footed ferrets were similar to movements of wild-born ferrets (Biggins et al., 1985), but were shorter and slower than moves of our Siberian polecats. Activity patterns of black-footed ferrets and Siberian polecats also were species-unique, and appeared to be endogenous, at least for ferrets. The adaptive value of the Siberian polecat activity pattern is unclear, but the pattern for black-footed ferrets seems advantageous for predator avoidance in the North American prairie dog ecosystem. Behaviors of ferret-polecat hybrids have not been closely examined, but any future attempt at genetic manipulation should proceed cautiously, and should involve experimental evaluations of behaviors in the laboratory and during trial releases of reproductively sterile animals.

Searches for black-footed ferrets are often conducted using spotlights at night (Campbell et al., 1984) to monitor survival rates of released animals (Biggins et al., 1998) and to conduct other studies. Ferrets spent about 92 % of their non-day hours

belowground in this study; it is important, therefore, to conduct searches when ferrets are most active. Efficiency of searches should be greatest in the early morning hours, and may be further enhanced by bright moonlight.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Alkon, P. U., and D. Saltz. 1988. Influence of season and moonlight on temporal activity patterns of Indian crested porcupines (Hystrix indica). Journal of Mammalogy 69:71-80.

Alldredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50:157-165.

_____, and _____. 1992. Further comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 56:1-9.

Andelt, W. F., and P. S. Gipson. 1979. Home range, activity, and daily movements of coyotes. Journal of Wildlife Management 43:944-951.

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.

Beltrán, J. F., and M. Delibes. 1994. Environmental determinants of circadian activity of free-ranging Iberian lynxes. Journal of Mammalogy 75:382-393.

Berg, W. E., and R. A. Chesness. 1978. Ecology of coyotes in northern Minnesota. Pp. 229-247 in M. Bekoff (ed.), Coyotes: Biology, Behavior, and Management. Academic Press, New York.

Berry, K. J., and P. W. Mielke, Jr. 1985. Subroutines for computing exact Chi-square and Fisher's exact probability tests. Education and Psychological Measurement 45:153-159.

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.

_____, M. H. Schroeder, S. C. Forrest, and L. Richardson. 1985. Movements and habitat relationships of radio-tagged black-footed ferrets. Pp. 11.1-11.17 in S. W. Anderson and D. B. Inkley (eds.), Black-footed Ferret Workshop Proceedings, Wyoming Game and Fish Department, Cheyenne.

_____, _____, _____, and _____. 1986. Activity of radio-tagged black-footed ferrets. Great Basin Naturalist Memoirs 8:135-140.

_____, 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.

Brom, I. P. 1954. Materials on the biology of the transbaikal polecat. Nauchno-Issledovatel'shogo Protivo-chumnogo Instituta Sibiri i Dalnego Vostoka 12:224-230.

Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76:408-415.

Campbell, T. M. III, D. Biggins, S. Forrest, and T. W. Clark. 1985. Pp. 24.1-24.7 in S. W. Anderson and D. B. Inkley (eds.), Black-footed Ferret Workshop Proceedings, Wyoming Game and Fish Department, Cheyenne.

Carothers, J. H., and F. M. Jaksić. 1984. Time as a niche difference: the role of interference competition. Oikos 42:403-406.

Clark, C. W., and D. A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist 131:271-290.

Clark, F. W. 1972. Influence of jackrabbit density on coyote population change. Journal of Wildlife Management 36:343-356.

Clark, T. W., L. Richardson, S. C. Forrest, D. E. Casey, and T. M. Campbell III. 1986. Descriptive ethology and activity patterns of black-footed ferrets. Great Basin Naturalist Memoirs 8:115-134.

Clarke, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (Asio flammeus) and deer mice (Peromyscus maniculatus). Behavioral Ecology and Sociobiology 13:205-209.

Cresswell, W. J., and S. Harris. 1988. The effects of weather conditions on the movements and activity of badgers (Meles meles) in a suburban environment. London Journal of Zoology 216:187-194.

Cypher, B. L., and K. A. Spencer. 1998. Competitive interactions between coyotes and San Joaquin kit foxes. Journal of Mammalogy 79:204-214.

Dano, L. E. 1952. Cottontail rabbit (Sylvilagus audubonibaileyi) populations in relation to prairie dog (Cynomys ludovicianus ludovicianus) towns. M.S. thesis, Colorado State University, Fort Collins.

Davison, A., J., D. S. Birks, H. I. Griffiths, A. C. Kitchener, D. Biggins, and R. K. Butlin. 1999. Hybridization and the phylogenetic relationship between polecats and domestic ferrets in Britain. Biological Conservation 87:155-161.

Debrot, S., J. M. Weber, P. Marchesi, and C. Mermod. 1985. The day and night activity pattern of the stoat (Mustela erminea L.). Mammalia 49:13-17.

Denisov, E. I. 1984. Study of the biology of steppe polecats in the period of raising the young. Izvestiya Sibirskogo Otdeleniya, Akad. Nauk SSSR, Seriya Biologicheskikh Nauk. 15(5):89-93.

Drew, G. S., and J. A. Bissonette. 1997. Winter activity patterns of American martens (Martes americana): rejection of the hypothesis of thermal-cost minimization. Canadian Journal of Zoology 75:812-816.

Ellis, R. J. and S. D. Schemnitz. 1958. Some foods used by coyotes and bobcats in Cimarron County, Oklahoma 1954 through 1956. Proceedings of the Oklahoma Academy of Sciences 38:180-185.

Fafarman, K. R., and R. J. Whyte. 1978. Factors influencing nightime roadside counts of cottontail rabbits. Journal of Wildlife Management 43:765-767.

Fenton, M. B., N. G. H. Boyle, T. M. Harrison, and D. J. Oxley. 1977. Activity patterns, habitat use, and prey selection by some African insectivorous bats. Biotropica 9:73-85.

Fichter, E., G. Schildman, and J. H Sather. 1955. Some feeding patterns of coyotes in Nebraska. Ecological Monographs 25:1-37.

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

Fuller, T. K., and L. B. Keith. 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. Journal of Mammalogy 62:403-405.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1989. Changes in coyote movements due to military activity. Journal of Wildlife Management 53:334-339.

Gilbert, B. S., and S. Boutin. 1991. Effect of moonlight on winter activity of snowshoe hares. Arctic and Alpine Research 23:61-65.

Gier, H. T. 1968. Coyotes in Kansas (revised). Kansas State College Agricultural Experiment Station Bulletin 393. 118 p.

Gliwicz, Z. M. 1986. A lunar cycle in zooplankton. Ecology 67:883-897.

Harris, S. W. 1974. Status, chronology and ecology of nesting storm-petrels in northern California. Condor 76:249-261.

Hanson, R. M.., and I. K. Gold. 1977. Blacktail prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. Journal of Range Management 30:210-214.

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.

Heptner, V. G., N. P. Naumov, P. B. Yurgenson, A. A. Sludskii, A. F. Chirkova, and A. G. Bannikov. 1967. Mammals of the Soviet Union: Sea Cows and Carnivores (Volume 2). Vysshaya Shkola, Moscow.

Hillman, C. N. 1968. Field observations of black-footed ferrets in South Dakota. Transactions of the North American Wildlife and Natural Resources Conference 33:433-443.

Hoffmann, R. S. and D. L. Pattie. 1968. A guide to Montana mammals. University of Montana, Missoula. 133 pp.

Holomuzki, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. Ecology 67:737-748.

Holt, R. D., and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics 25:495-520.

_____, and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149:745-764.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

Jaksić, F. M. 1982. Inadequacy of activity time as a niche difference: the case of diurnal and nocturnal raptors. Oecologia 52:171-175.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Johnson, J. K., and R. M. Hansen. 1979. Coyote food habits on the Idaho National Engineering Laboratory. Journal of Wildlife Management 43:951-956.

Joshi, A. R., J. L. David Smith, and F. J. Cuthbert. 1995. Influence of food distribution and predation pressure on spacing behavior in palm civets. Journal of Mammalogy 76:1205-1212.

Kaufman, D. W. and G. A. Kaufman. 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (Dipodomys ordii). Journal of Mammalogy 63:309-312.

Kolb, H. H. 1992. The effect of moonlight on activity in the wild rabbit (Oryctolagus cuniculus). London Journal of Zoology 228:661-665.

Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. Ecology 65:689-701.

_____, J. S. Brown, and O. Hasson. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249-2260.

_____, _____, R. J. Smith, and W. O. Wirtz II. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. Oikos 53:145-152.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecology 67:760-770.

Kydyrbaev, Kh. K. 1988. Ecology of the Siberian polecat in Kazakhstan. Trudy Akad. Nauk KazSSR, Ser. In-ta Zool. 44:56-68.

Laundré, J. W., and B. L. Keller. 1981. Home-range use by coyotes in Idaho. 1981. Animal Behaviour 29:449-461.

Lechleitner, R. R. 1958. Movements, density and mortality in a black-tailed jackrabbit population. Journal of Wildlife Management 22:371-384.

Lepitzki, D. A. W. 1990. Summer and fall activity patterns of cottontail rabbits, Sylvilagus floridanus, in southern Illinois. Canadian Field Naturalist 104:552-556.

Lima, S. L. 1988. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. Oikos 53:3-11.

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.

Lockard, R. B., and D. H. Owings. 1974a. Moon-related surface activity of bannertail (Dipodomys spectabilis) and Fresno (D. nitratoides) kangaroo rats. Animal Behavior 22:262-273.

_____, and _____. 1974b. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. Journal of Mammalogy 55:189-193.

Lode, T. 1995. Activity pattern of polecats Mustela putorius L. in relation to food habits and prey activity. Ethology 100:295-308.

Lord, R. D. 1964. Seasonal changes in the activity of penned cottontail rabbits. Animal Behaviour 12:38-41.

Maccracken, J. G., and R. M. Hansen. 1987. Coyote feeding strategies in southeastern Idaho: optimal foraging by an opportunistic predator. Journal of Wildlife Management 51:278-285.

McClean, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. Journal of Wildlife Management 62:793-801.

Mech, L. D., K. L. Heezen, and D. B. Siniff. 1966. Onset and cessation of activity in cottontail rabbits and snowshoe hares in relation to sunset and sunrise. Animal Behaviour 14:410-413.

Meinzer, W. P., D. N. Ueckert, and J. T. Flinders. 1975. Foodniche of coyotes in the rolling plains of Texas. Journal of Range Management 28:22-27.

Miller, B. J., and S. H. Anderson. 1990. A comparison between black-footed ferrets (Mustela nigripes), domestic ferrets (M. putorius furo), and Siberian polecats (M. eversmanni). Zoo Biology 9:201-210.

_____, and _____. 1993. Descriptive ethology of the endangered black-footed ferret. Advances in Behavior (Series), Paul Parey Press, Berlin, Germany.

_____, B., R. P. Reading, and S. Forrest. 1996. Prairie night. Smithsonian Institution Press, Washington, D.C.

Morrison, D. W. 1978. Lunar phobia in a neotropical fruit bat, Artibeus jamaicensis (Chiroptera: Phyllostomidae). Animal Behaviour 26:852-855.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models--fourth edition. Irwin, Inc., Chicago.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541-545.

Nowak, R. M. 1978. Evolution and taxonomy of coyotes and related Canis. Pp. 3-16 in M. Bekoff (ed.), Coyotes: Biology, Behavior, and Management. Academic Press, New York.

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. Pages 21-33 in U. S. Seal, E. T. Thorne, M. A. Bogan, and S. H. Anderson (eds.), Conservation biology and the black-footed ferret. Yale University Press, New Haven, CT.

O,Donoghue, M., S. Boutin, C. J. Krebs, and E. J. Hofer. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. Oikos 80:150-162.

O'Donoghue, M. O., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology 79:1193-1208.

Paunovich, R., and S. C. Forrest. 1987. Activity of a wild black-footed litter. Prairie Naturalist 19:159-162.

Paquet, P. C. 1991. Winter spatial relationships of wolves and coyotes in Riding Mounatin National Park, Manitoba. Journal of Mammalogy 72:397-401.

_____. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy 73:337-343.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20:297-330.

Price, M. V., N. M. Waser, and T. A. Bass. 1984. Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65:353-356.

Richardson, L., T. W. Clark, S. C. Forrest, and T. M. Campbell III. 1987. Winter ecology of black-footed ferrets (Mustela nigripes) at Meeteetse, Wyoming. American Midland Naturalist 117:225-239.

Rogowitz, G. L. 1997. Locomotor and foraging activity of the whit-tailed jackrabbit (Lepus townsendii). Journal of Mammalogy 78:1172-1181.

Rydell, J., A. Entwistle, and P. A. Racey. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos 76:243-252.

Saltz, D., and P. U. Alkon. 1985. A simple computer-aided method for estimating radio-location error. Journal of Wildlife Management 49:664-668.

Sandell, M. 1989. Ecological energetics, optimal body size and sexual size dimorphism: a model applied to the stoat, Mustela erminea L. Functional Ecology 3:315-324.

Serrebrennikov, M. K. 1929. The steppe polecat (Putorius eversmanni) in the Wermut steppes of northern Kazakhstan. Zeithschrift für Säugetierkunde 4:205-212.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pp. 203-224 in W. C. Kerfoot and A. Sih (eds.), Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.

Smith, G. W. 1990. Home range and activity patterns of black-tailed jackrabbits. Great Basin Naturalist 50:249-256.

Soulé, M. E., D. 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.

Spiller, D. A., and T. W. Schoener. 1990. A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. Nature 347:469-471.

Stangel, P. W., and R. D. Semlitsch. 1987. Experimental analysis of predation on the diel vertical migrations of a larval salamander. Canadian Journal of Zoology 65:1554-1558.

Stephenson, R. O., D., V. Grangaard, and J. Burch. 1991. Lynx, Felis lynx, predation on Red Foxes, Vulpes vulpes, Caribou, Rangifer tarandus, and Dall Sheep, Ovis dalli, in Alaska. Canadian Field Naturalist 105:255-262.

Stewart, R. W., and J. R. Bider. 1977. Summer activity of muskrats in relation to weather. Journal of Wildlife Management 41:487-499.

Stroganov, S.U. 1962. Carnivorous Mammals of Siberia. Translation: Israel Program for Scientific Translations, Jerusalem, 1969. U.S. Dept. Commerce, Clearinghouse for Federal Scientific and Technical Information, Springfield, Virginia 22151.

Sviridenko, P. A. 1935. The steppe polecat (Putorius eversmannii) and its agricultural importance in the control of rodents. Izdatel'stvo VASKhNIL, Moskva-Leningrad. 151 p. (translation).

Swihart, R. K., and N. A. Slade. 1985. Testing for independence of observations in animal movements. Ecology 66:1176-1184.

Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322-330.

Thurber, J. M., R. O. Peterson, J. D. Woolington, and J. A. Vucetich. 1992. Coyote coexistence with wolves on the Kenai Peninsula, Alaska. Canadian Journal of Zoology 70:2494-2498.

U. S. Navy. 1999. Table of sunrise/sunset, moonrise/moonset, or twilight times for an entire year. U. S. Naval Observatory, Astronomical Applications Department, Data Services. Http://aa.usno.navy.mil/AA/data.

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.

Vargas, A., and S. H. Anderson. 1998. Black-footed ferret (Mustela nigripes) behavioral development: aboveground activity and juvenile play. Journal of Ethology 16:29-41.

Vickery W. L., and J. R. Bider. 1978. The effect of weather on Sorex cinerius activity. Canadian Journal of Zoology 56:291-299.

Villablanca, F. X. 1996. Conservation genetics of the black-footed ferret I: a phylogenetic perspective. In Abstracts of the American Society of Mammalogists 1996 Annual Meeting.

Villafuerte, R., M. B. Kufner, M. Delibes, and S. Moreno. 1993. Environmental factors influencing the seasonal daily activity of the European rabbit (Oryctolagus cuniculus) in a Mediterranean area. Mammalia 57:341-347.

Watanuki, Y. 1986. Moonlight avoidance behavior in Leach's storm-petrels as a defense against slaty-backed gulls. Auk 103:14-22.

Wells, M. C., and P. N. Lehner. 1978. The relative importance of the distance senses in coyote predatory behaviour. Animal Behaviour 26:251-258.

White, G. C., and R. A. Garrott. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.

Williams, E. S., E. T. Thorne, M. J. G. Appel, and D. W. Belitsky. 1988. Canine distemper in black-footed ferrets (Mustela nigripes) from Wyoming. Journal of Wildlife Diseases 24:385-398.

Woodruff, R. A., and B. L. Keller. 1982. Dispersal, daily activity and home range of coyotes in southeaster Idaho. Northwest Science 56:199-207.

Zverev, M. D. 1931. Materials on biology and agricultural importance in Siberian of the polecat and other small predators of the family Mustelidae. Proceedings of the Institute for Plant Protection of Siberia 1 (8).

Zhou, W., W. Wanhong, and D. E. Biggins. 1994a. Study on population dynamic of polecats and its effective factors. Acta Biologica Plateau Sinica 12:161-171.

_____, _____, and _____. 1994b. Activity rhythm of polecat in Qing-zang Plateau. Acta Biologica Plateau Sinica 12:173-187.

_____, _____, and _____. 1995. Activity rhythms and distribution of natal dens for red foxes. Acta Theriologica Sinica 15:267-272.

Zielinski, W. J., W. D. Spencer, and R. H. Barrett. 1983. Relationship between food habits and activity patterns of pine martens. Journal of Mammalogy 64:387-396.

Table 4.1. Comparisons, measures used, and analysis methods for assessing effects of time of day and moonlight on activities of black-footed ferrets and Siberian polecats.

Primary Comparison	Measure of Activity	Data Subset	Unit of Observation	Attribute	Analysis Method
Polecat vs. Ferret	Location-based	All Data	Animal	Rate of Movement	MGLM[1]
Day vs. Non-day	PI-based	All Data (by species)	Bout	Count	Availability vs. Use[2]
4 Non-day Periods	Location-based	Non-day (by species)	Bout Animal	Count Total Movement	Availability vs. Use[2] Descriptive
Moon vs. No Moon	Location-based	Night (by species); "Complete" Nights	Bout Animal	Count Total Movement	Availability vs. Use[2] Descriptive
		Night (by species); "Partial" Moon	Bout Animal	Count Total Movement	Availability vs. Use[2] Descriptive
Amount of Moon Illumination	Location-based	Night (by species) Illumination ≥20%	Bout	Movement	MGLM[1]

[1]Multivariate General Linear Modeling using Analysis of Variance
[2]Neu et al., 1974

Table 4.2. Categorical divisions of the calendar day for summarizing cumulative telemetric monitoring time and activity of black-footed ferrets and Siberian polecats.

Period # & description	Begin	End
0 Day	Sunrise + 0.5 h	Sunset - 0.5 h
1 Crepuscular PM	Sunset - 0.5 h	Sunset + 1.0 h
2 Evening	Sunset + 1.0 h	Sunset + 2.0 h
3 Pre-midnight	Sunset + 2.0 h	Midnight
4 Post-midnight	Midnight	Sunrise - 2.0 h
5 Morning	Sunrise - 2.0 h	Sunrise - 1.0 h
6 Crepuscular AM	Sunrise - 1.0 h	Sunrise + 0.5 h

Table 4.3. Summary of cumulative monitoring time, cumulative movements, and number of bouts of activity for black-footed ferrets and Siberian polecats released during 1989-1991 on prairie dog colonies.

	BLACK-FOOTED FERRETS			SIBERIAN POLECATS		
Cagegory:	Monitor (h)	Movement (km)	Bouts (n)	Monitor (h)	Movement (km)	Bouts (n)
Day (Per. 0)	2284	0.8	2	425	31.5	15
Twilight PM (Per. 1+2)	549	9.2	20	150	14.2	17
Night PM (Per. 3)	968	34.0	68	342	24.1	18
Night AM (Per. 4)	905	62.5	98	308	28.5	27
Twilight AM (Per. 5+6)	539	16.2	13	146	13.4	12
Total	5245	122.7	201	1371	111.7	89
Moon: (In Per. 2-5):						
Moonlit Nights	445	30.9	55	91	23.5	8
Dark Nights	551	18.9	46	120	3.1	5
Mixed Nights	1350	62.8	85	564	41.6	45

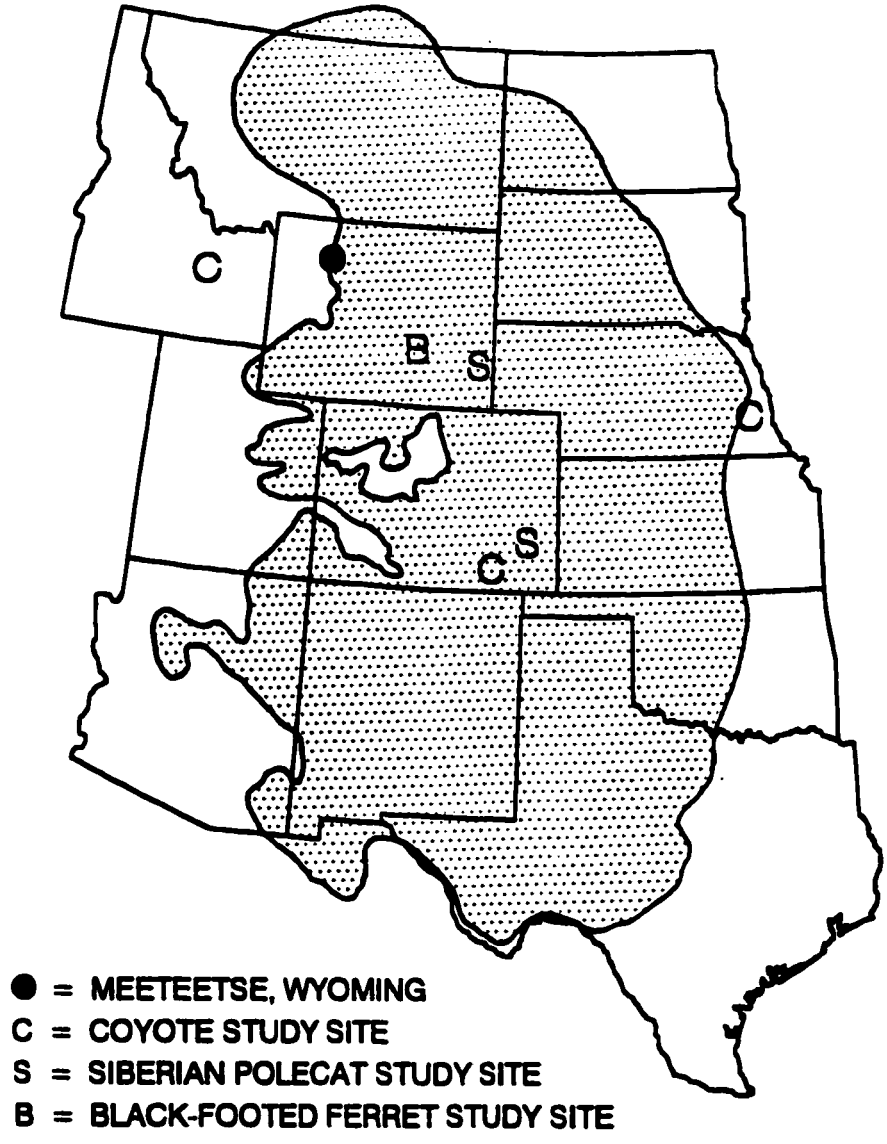

Figure 4.1. Probable historic range of black-footed ferrets in western North America as defined by composite ranges (stippled area) of Cynomys ludovicianus, C. leucurus, and C. gunnisoni (modified from Miller et al., 1996), study areas where polecats and black-footed ferrets were released, study areas where telemetric data on coyotes were available (studies of Andelt and Gipson, 1979; Gese et al., 1989; Laundré and Keller, 1981; and Woodruff and Keller, 1982), and the location of the extirpated population of ferrets ancestral to all captive and released animals (Meeteetse, Wyoming).

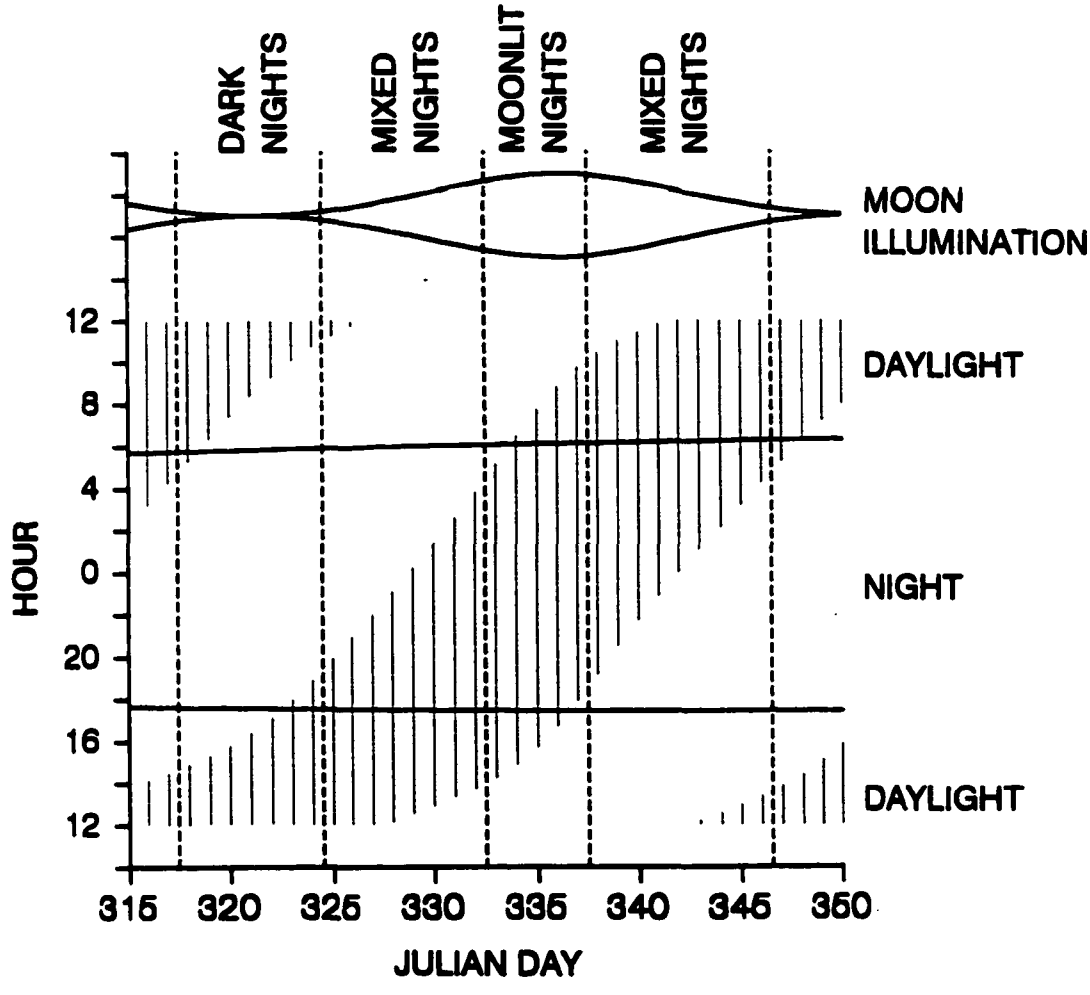

Figure 4.2. Example of moon cyclicity during a portion of the Siberian polecat study in 1990. A day extends from noon of the Julian day indicated until noon of the following day, with vertical lines showing duration of moonlight. Night extends from sunset + 1 h until sunrise - 1 h. Relative moon illumination (0% - 100%) is defined by the space between the converging and diverging curves near the top of the graph. "Dark" nights were those with < 1.5 h of moonlight available, "moonlit" nights had < 1.5 h without moonlight, and "mixed" nights were the remainder.

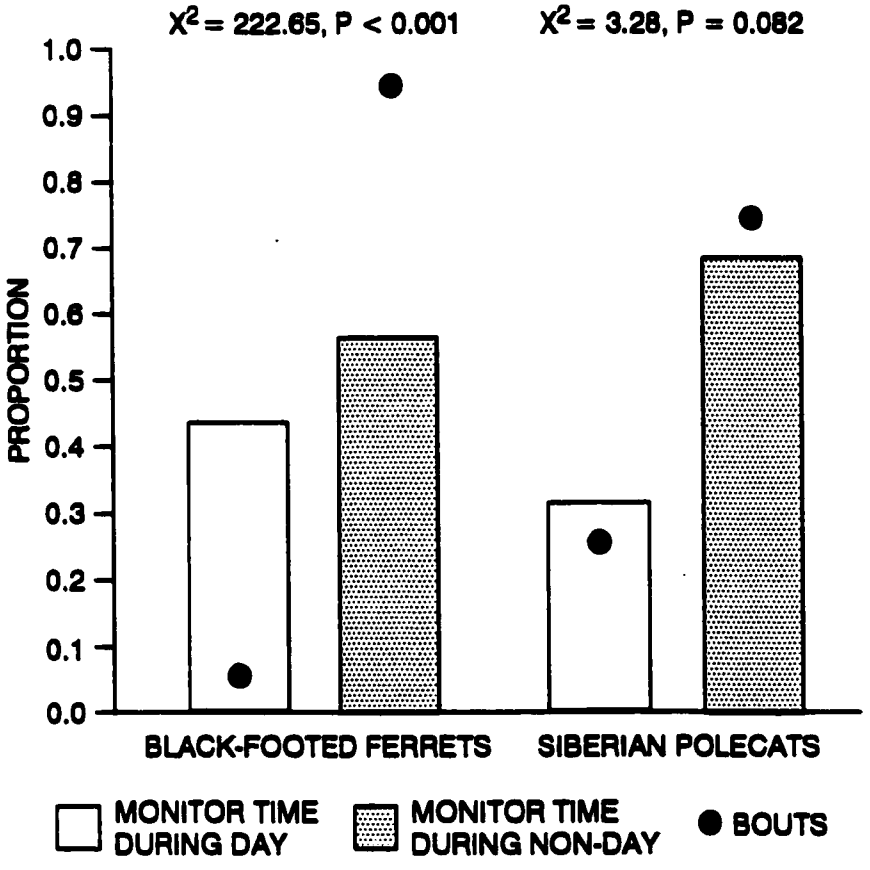

Figure 4.3. Proportionate use (pulse interval based bouts of activity) during day and non-day periods by black-footed ferrets and Siberian polecats compared to availability (cumulative pulse interval based telemetric monitoring time) within those periods. Chi-square values and probabilities refer to numbers of bouts compared to monitoring time in periods.

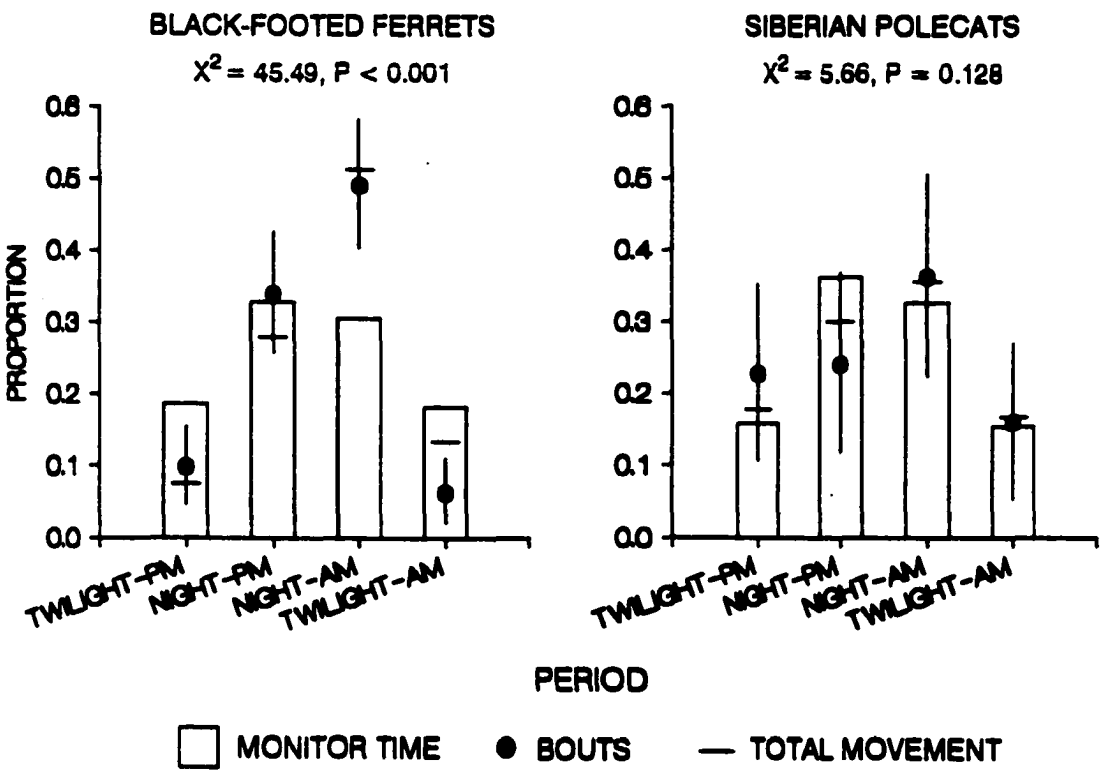

Figure 4.4. Use (bouts of activity, total movement) of 4 non-day categories by black-footed ferrets and Siberian polecats compared to availability (cumulative telemetric monitoring time) within those categories. Chi-square values and probabilities refer to the omnibus tests comparing number of bouts with monitor time. Proportions of bouts are bounded by 95% (Bonnferroni-adjusted) confidence intervals; intervals within boxes indicate significant avoidance and the interval above the box indicates significant selection for activity during that category. Categories are delimited as follows (sunset-0.5 h) < "TWILIGHT-PM" < sunset+2.0 h < "NIGHT-PM" < midnight < "NIGHT-AM" < sunrise-2.0 h < "TWILIGHT-AM" < sunrise+0.5 h.

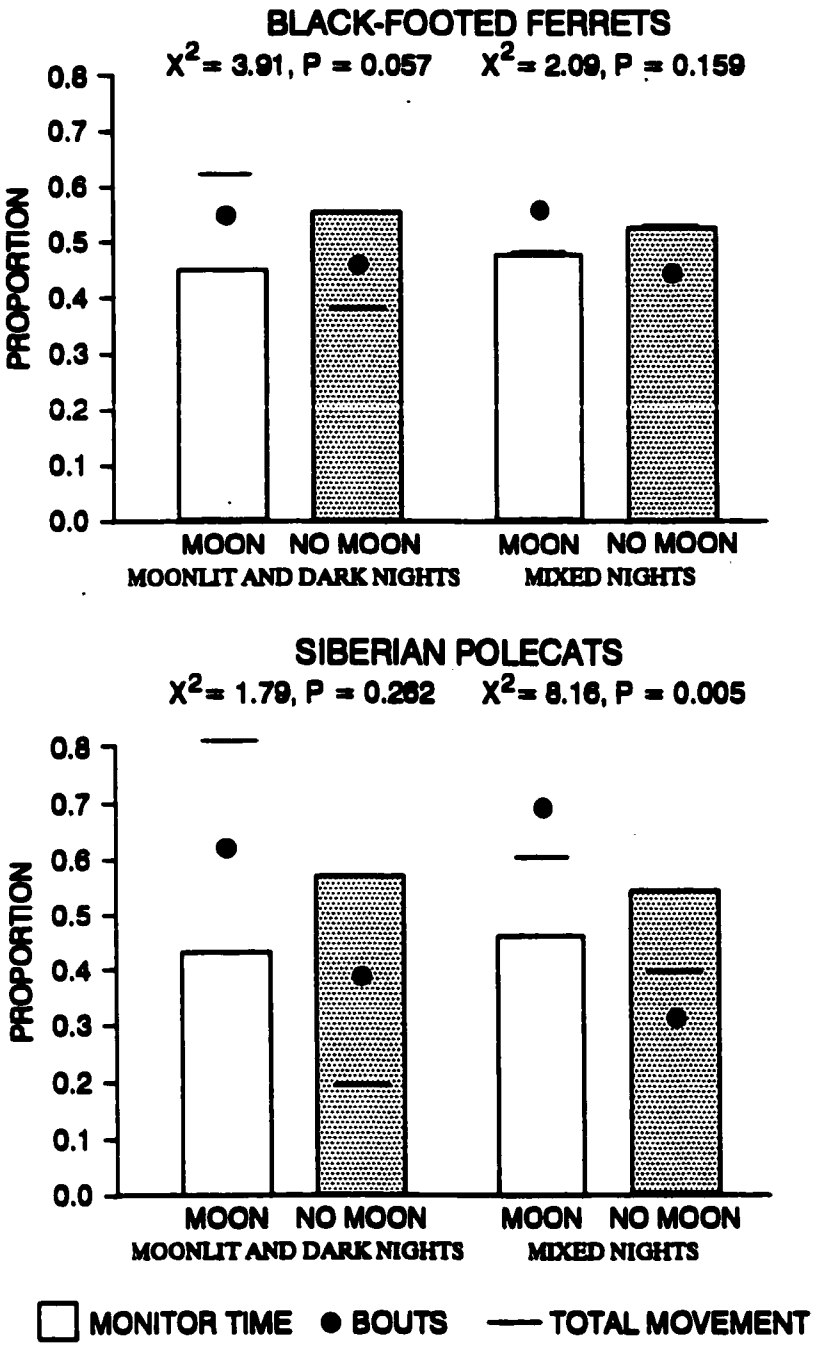

Figure 4.5. Proportionate use (bouts of activity) in moonlit and non-moonlit periods by black-footed ferrets and Siberian polecats compared to proportionate availability (cumulative telemetric monitoring time) within those periods. Chi-square values and probabilities refer to numbers of bouts compared to monitoring time in periods.

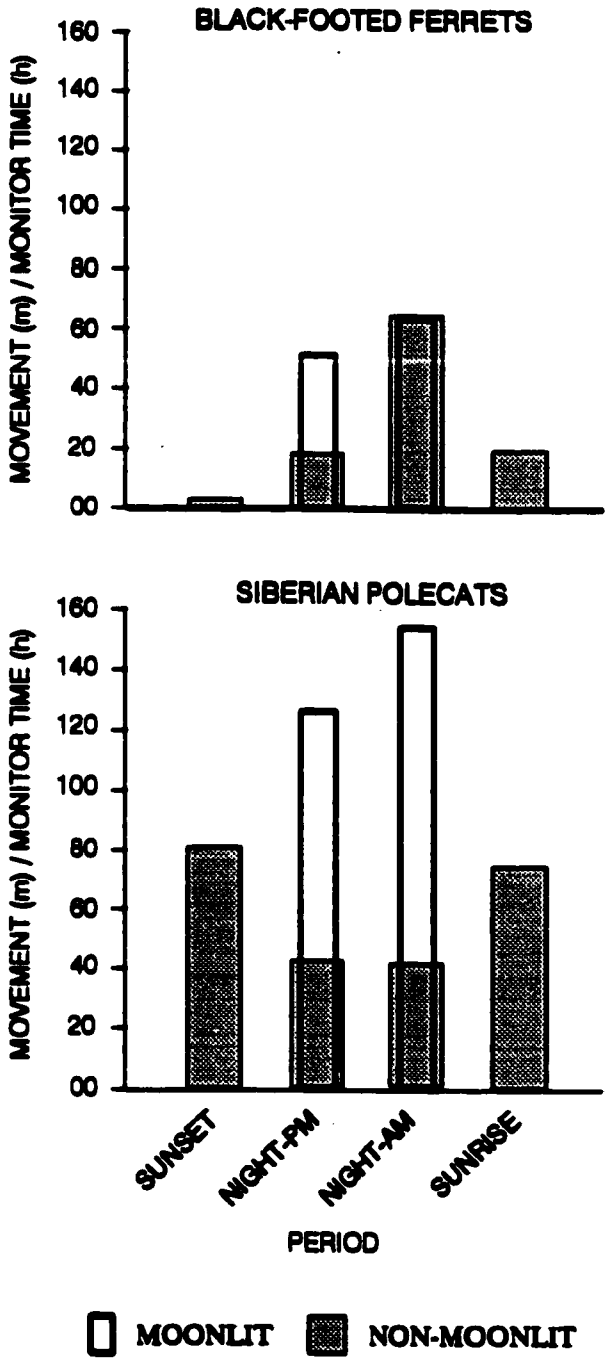

Figure 4.6. Combined effects of moon and time category on movement rates of black-footed ferrets and Siberian polecats. Categories were delimited as follows: sunset-0.5 h < "SUNSET" < sunset+1.0 h < "NIGHT-PM" < midnight < "NIGHT-AM" < sunrise-1.0 h < "SUNRISE" < sunrise+0.5 h.

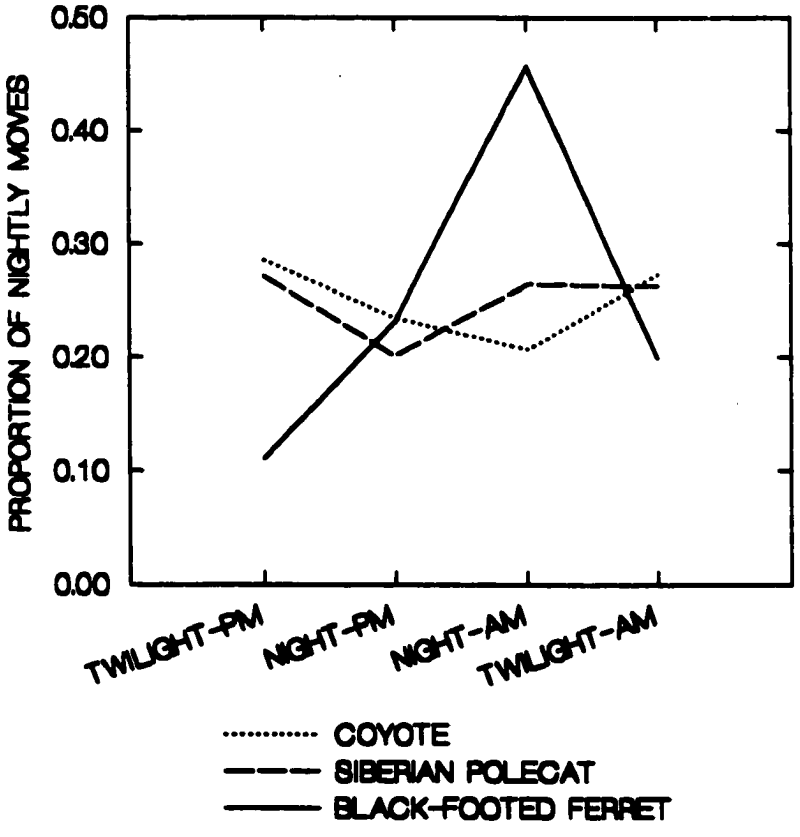

Figure 4.7. Relative movements of black-footed ferrets, Siberian polecats, and coyotes in 4 non-day categories, expressed as a proportion of total movement (adjusted by monitor time) for each species in all 4 categories. Categories are delimited as follows (sunset-0.5 h) < "TWILIGHT-PM" < sunset+2.0 h < "NIGHT-PM" < midnight < "NIGHT-AM" < sunrise-2.0 h < "TWILIGHT-AM" < sunrise+0.5 h. Coyote data were extracted from Andelt and Gipson (1979), Gese et al.(1989), Laundré and Keller (1981), and Woodruff and Keller (1982).

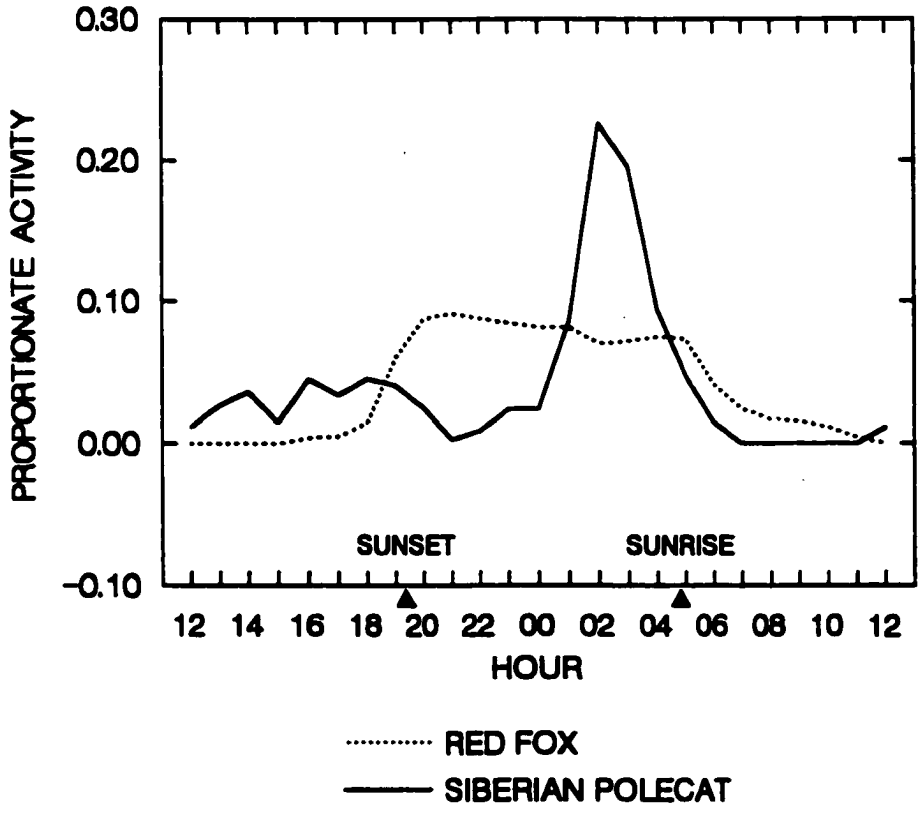

Figure 4.8. Activity of Siberian polecats and red foxes in Qinghai Province, China, during summer. Data were extracted from Zhou et al. (1994b) and Zhou et al. (1995).

CHAPTER 5

THE EFFECT OF REARING METHODS ON SURVIVAL OF REINTRODUCED BLACK-FOOTED FERRETS[1]

Abstract: Minimum survival rates were estimated for 282 young-of-year, captive-reared, black-footed ferrets (*Mustela nigripes*) reintroduced into prairie dog (*Cynomys* spp.) colonies in Wyoming, Montana, and South Dakota. We used night surveys with spotlights to locate ferrets about 1 month and 9 months postrelease. We modeled minimum survival rates using gender, year, site, and 4 rearing methods. Minimum survival rates were highest (30% for 1 month, 20% for 9 months) for ferrets reared from early ages in outdoor pens with simulated prairie dog habitat; survival was lowest for cage-reared ferrets released without pen experience (11% for 1 month, 2% for 9 months). Rearing method and year influenced 1-month survival in a comparison of 3 levels of pen experience (pen rearing as defined above, transfer of kits from zoos to pen facilities at age 60-90 d, and transfer at age >90 d) during releases in 1994-95 in Montana. Higher survival was associated with intensive management of coyotes (*Canis latrans*) in 1995.

---

[1] This chapter has been published as Biggins, D. E., J. L. Godbey, L. R. Hanebury, B Luce, P. E. Marinari, M.. R. Matchett, and A. Vargas. 1998. The effect of rearing methods on survival of reintroduced black-footed ferrets. *Journal of Wildlife Management 62:643-653.*

Survival was not significantly different ($P>0.05$) between sites or sexes, regardless of model. We recommend routine use of outdoor pens for prerelease conditioning of black-footed ferret kits.

The endangered black-footed ferret (*Mustela nigripes*) is a 600-1,200 g mustelid dependent on prairie dogs for food and shelter. The ferret's decline was linked to the reduction in prairie dogs, which were widely eradicated as a prairie pest, but diseases also may have played an important role (Biggins and Schroeder 1988). The prognosis for recovery of the black-footed ferret was bleak after failure of the first captive-propagation attempt in the early 1970s (Carpenter 1984), which was accompanied by loss of the wild populations in South Dakota that supplied the breeding stock. Hope for the black-footed ferret was renewed in 1981 by discovery of another population near Meeteetse, Wyoming. That population thrived until 1985, when 2 diseases, canine distemper and plague (*Yersinia pestis*), struck the ferrets, and plague began causing widespread reductions in the white-tailed prairie dog (*Cynomys ludovicianus*) population on which the ferrets depended (Forrest et al. 1988, Williams et al. 1988). These events transformed the orderly initiation of a captive-breeding program into an emergency rescue effort (Miller et al. 1996). Successful captive propagation expanded the 18 ferrets salvaged from Meeteetse into a population of 250-300 breeders with sufficient surplus to sustain annual reintroductions since 1991.

Predation caused most loss of neutered Siberian polecats (*Mustela eversmannii*) released onto prairie dog colonies during initial tests of strategies to be used on ferrets.

Within 6 weeks of release, 81% of 52 captive-reared polecats had been killed by predators: 56% by coyotes, 23% by badgers (*Taxidea taxus*), and 2% by avian predators, but only 1 of 5 wild-caught polecats translocated from China was lost to predation (D. Biggins et al., Trial release of Siberian polecats, progress reports, Midcontinent Ecological Science Center, Fort Collins, Colo., 1990-91). Polecats improved their predator avoidance skills when aversively conditioned in laboratory trials (Miller et al. 1990), but aversive conditioning has not been used on black-footed ferrets. Coyotes, badgers and avian predators have continued to cause losses of ferrets during reintroductions (Miller et al. 1994, Vargas 1994).

Early experience of animals in natural or complex environments can affect the development of predation-avoidance behaviors and other skills. Mongolian gerbils (*Meriones unguiculatus*) reared in quasi natural burrow systems were significantly more responsive to a threat stimulus than were gerbils reared in cages without shelter (Clark and Galef 1977), and domestic rats (*Rattus norvegicus*) with early postweaning experience in "enriched" environments were more active (Huck and Price 1975) and showed more rapid escape responses from a predator model (Renner 1988) when compared to rats from unenriched cages. Environmental influences on behaviors may be correlated to changes in brain structure (Greenough and Juraska 1979, Rosenzweig 1979).

Potential benefits of early experience by black-footed ferrets in soil-filled pens with burrows include (1) decreased habituation to human caretakers (less care is needed); (2) opportunity to hunt and kill prairie dogs in burrows (Vargas 1994); (3) increased physical conditioning afforded by greater space; (4) increased physiological conditioning by

exposure to soil microorganisms, including some known pathogens; (5) opportunity to dig; (6) decreased exposure to stressful stimuli (e.g., noise) by dwelling in burrows; (7) conditioning on burrows as the appropriate refuge from many hazards; and (8) increased opportunity to practice play behaviors, which may affect later social skills and predatory efficacy (Vargas 1994).

Our goal was to increase the proportion of released black-footed ferrets surviving to reproductive age, primarily by reducing losses to other predators. In 1992-95, we tested the working hypothesis that early experience in a quasi natural setting will affect postrelease survival of black-footed ferrets.

METHODS

Rearing Strategies

Producers maintained some ferrets (the CAGE group) in indoor cages until release. The typical cage was made of plywood and vinyl-coated welded wire (1.27 cm mesh), with floor area 1.22 m × 1.22 m, and height 0.61 m. Cages were elevated approximately 1 m above floor level, with a floor-level nest box connected to the cage by a plastic tube (10-cm diameter) and a second box attached directly to the cage. The standard diet for cage-held animals was a mixture of 40% ground rabbit (*Oryctolagus cuniculus*) or prairie dog meat and 60% commercial mink chow. The CAGE ferrets were given live hamsters (*Mesocricetus auratus*) once per week, and were given prairie dog portions approximately twice per week after reaching an age of 60 days.

We tested 3 additional rearing methods that involved placement of juvenile ferrets in quasi natural enclosures for varying periods of time before release on wild prairie dog

habitat. The pen enclosures varied in size from 18 to 280 m^2, were filled with soil 1.2-2.4 m in depth, and were stocked with prairie dogs to construct burrow systems. Pens were at the Wyoming Game and Fish Department's ferret production facility (now the U.S. Fish and Wildlife Service's National Black-footed Ferret Conservation Center), Sybille, Wyoming, and the U.S. Fish and Wildlife Service's (later National Biological Service's) Ferret Research Facilities at the Pueblo Army Depot in Colorado and F.E. Warren Air Force Base in Wyoming. Sybille pens supplied kits for release in Wyoming and South Dakota, and kits from Warren and Pueblo pens were released in Montana.

Kits produced and conditioned at these sites were termed pen-residents (PENRES) and were preconditioned by placing them as family groups (with dams) in pens ≥ 75 m^2. Some PENRES females whelped in cages placed in pens and were allowed access to pens when kits were 28-60 days old. Other females whelped in nest boxes buried in their pens and were allowed almost immediate access to burrows. No dam was permitted to whelp in a prairie dog burrow, which may be beneficial, but would have precluded most monitoring of newborn young. Our first tests of conditioning compared these relatively experienced PENRES animals with the most naive CAGE animals.

Two additional levels of preconditioning tested in Montana during 1994-95 involved conditioning of kits referred to as transient because they were moved from the facility of birth to pens at Pueblo or Warren for the preconditioning period. Louisville Zoo and Metro Toronto Zoo produced kits shipped to Warren and Pueblo pens for conditioning in 1994. In 1995, ferret kits conditioned at experimental facilities came from Louisville Zoo, National Zoo (Washington D.C.), Henry Doorly Zoo (Omaha, Nebr.),

Phoenix Zoo, Cheyenne Mountain Zoo (Colorado Springs, Colo.) and Sybille. Ferrets were kept in sibling groups for conditioning and were of two general classes: (1) family groups that included the dam and were transferred to pen facilities when kits were ≥60 ($\bar{x}$ = 74) days old (PEN60), and (2) kits shipped without dams at >90 ($\bar{x}$ = 101) days of age (PEN90). Mean duration of residence of kits in pens was 99 days for PENRES kits, 80 days for PEN60 kits, and 51 days for PEN90 kits.

We fed prairie dogs to ferrets held in pens, although occasional substitutions of rabbit and mink chow were used when prairie dogs were unavailable. The PENRES females generally were accustomed to killing prairie dogs and were fed mostly live prey during the kit-rearing period. Although live prairie dogs resided in some pens before ferrets were delivered, transient ferrets often made a more gradual transition to live prairie dogs by being given prairie dog portions or whole dead prairie dogs before being provided with live prairie dogs. The schedule of dietary transition for transients was variable, depending on killing skills of dams and kits and availability of prairie dogs.

We did not quantify frequency and duration of contact between ferrets and their human caretakers, but contact was undoubtedly greater in the cage environment than in the pen environments. Caretakers cleaned cages every 1-3 days, depending on facility, time of year, and presence of litters. Pens required no cleaning, except when subsurface nest boxes were used by ferrets. Multiple cages in 1 room also increased potential contact between humans and ferrets because caretakers were present until the last animals were fed and cleaned, and aisles between cage rows were often traversed repeatedly. Because

of the greater sizes of outdoor pens and differing access, close encounters (< 1-m separation) between caretakers and ferrets were less frequent.

Before shipment to a release site, we marked ferrets with ear tattoos (Fagerstone et al. 1985) and with passive integrated transponder (PIT) chips implanted subcutaneously behind the ear (Fagerstone and Johns 1987). Ferrets were shipped to reintroduction sites by truck (Wyoming and South Dakota), or by a combination of light aircraft and truck to the more remote site in Montana. Care and handling of ferrets was judged to be in full compliance with the Animal Welfare Act of 1985 during several reviews by institutional animal care and use committees.

Release

Our analyses used data from 282 captive-reared, young-of-year black-footed ferrets released in 3 states over a 5-year period (Table 5.1). Ferrets were released in August-November when they were 93-199 days old. Release strategies varied between sites and among years within sites. We held animals at release sites for a prerelease acclimation period of 9-14 days (all Wyo. and some S.D. animals), for a 1-day postshipping recovery period (Mont., 1994), or release on arrival (Mont., 1995). Accommodations for on-site acclimation were aboveground cages (on 1-m legs) and nest boxes (Wyo.) or ground-level cages with nest boxes buried belowground (all sites). We often provided acclimated animals with postrelease support in the form of continued access (for varying periods of time) to the release cage for refuge, water, and food.

Within each reintroduction site, characteristics of specific release locations had potential to influence ferret survival (e.g., variations in prairie dog density, density of

alternate prey, predator density, juxtaposition of other prairie dog colonies, proximity of dispersal barriers, distribution of human disturbances, presence of resident ferrets). We attempted to distribute potential influences of these variables equally among rearing groups by releasing similar numbers of animals from each rearing category at each specific release location during the Montana releases and the 1992 release in Wyoming. Although there was less emphasis on the distribution of sources of variation among treatment groups in Wyoming, 1993, and in South Dakota, 1994, examination of data revealed no associations that would confound interpretation; these datasets were considered to be sufficiently similar in methodology to warrant inclusion in the analyses.

Monitoring

We located ferrets at night via spotlights of 10^5-10^8 candle power that were operated from trucks, all-terrain vehicles (ATV), or by observers on foot (Clark et al. 1983, Campbell et al. 1985). Spotlight searches involved 8-32 people working singly on foot or on ATVs, and singly or in pairs from trucks. Each person or crew covered approximately 130 ha of prairie dog colony. Because ferrets can remain inactive belowground for several nights (Biggins et al. 1986, Richardson et al. 1987), each area was searched ≥3 consecutive nights. We attempted to uniformly search all parts of each prairie dog colony, regardless of perceived habitat quality or other factors.

We also attempted to individually identify all animals. In 1991-93, ferrets were captured for identification (Thorne et al. 1985). In 1994-96, we identified most ferrets remotely, via a custom-designed automated reader. The external loop antenna of the

reader was placed around the entrance of a burrow at which a ferret was seen, and the ferret's PIT tag was read if it approached within 10 cm.

The first survey was accomplished at about 1 month postrelease to assess short-term minimum survival. Additional animals detected later were treated as short-term survivors because they likely were present but undetected during the earlier survey, but only 5 such animals were added (9% of the sample). Because ferrets at each site during each year were released in subgroups several weeks apart, individuals had been free-ranging for varying periods of time when surveys were initiated. Furthermore, spotlighting in Wyoming and South Dakota was initiated about 30 days after the midpoint of releases, but spotlighting in Montana began 30 days after release of the last subgroup.

Data were available from surveys done in the summers (Jul-Aug) following fall releases in 1992 (Wyo.) and 1994 (Mont. and S.D.) to assess long-term minimum survival. Data from Wyoming surveys in summers of 1992 and 1994, and fall 1994 were not used because most ferrets were not individually identified.

Statistical Procedures

Maintaining a balanced design was important, and required different subsets of the data for analysis of key variables. No cell of a design was allowed to be vacant. For example, we required a year-site dataset to contain all treatment groups under consideration for a specified analysis. All subsets contained both genders, which allowed effect of gender to be assessed in all analyses. Thus, 4 analyses were conducted using the nonindependent subsets of data.

The PENRES versus CAGE comparisons allowed use of the 1992-94 short-term recapture data from Wyoming, Montana, and South Dakota, but excluded data from 1991 (no PENRES animals) and 1995 (no CAGE animals). We used short-term recapture data from the 2 years in Montana to assess the 3 types of conditioning: PENRES, PEN60, and PEN90. We conducted an additional analysis of short-term recapture data for CAGE animals in 1991-94, to evaluate gender differences. Finally, we compared PENRES and CAGE ferrets via long-term return data from Wyoming (1992-93), Montana (1994), and South Dakota (1994).

Because short-term and long-term analyses are necessarily based on animals from the same releases, the results are not independent. Nevertheless, we chose to maintain separate analyses for these time periods, rather than incorporate them into a single model with a temporal variable, primarily because of balanced design considerations and unequal time intervals between surveys.

Our multiple datasets involved 3 categorical variables (year-site, gender, rearing category). We conducted multivariate evaluations with program SURVIV (White 1983), using the approach of reducing the most general model (greatest number of estimable parameters) to the most parsimonious version that explains significant variation (Lebreton et al. 1992). Parameters in our analyses were estimable using algebraic formulae, but we used maximum likelihood estimates (MLE) from the iterative numerical optimization of program SURVIV. In addition to the initial release, at least 2 recapture sessions are required to attempt separation of recapture rate from survival rate (the f and S of Brownie et al. 1985). Although we had 2 such sessions for some releases, the second (summer)

session was absent or compromised in others, and the time intervals between sessions were unequal. Thus, we resorted to analyzing the product of the 2 rates (*Sf*), the "return rate" commonly referenced in bird banding studies or the minimum number known alive (MNA) of Krebs (1966). The limitation to considerations of return rate precluded any testing of equality of capture rates and reduced our ability to make inferences regarding population dynamics in ferrets, but that limitation had less effect on assessing differences between primary treatment groups.

Reiterating the philosophy of Lebreton et al. (1992), we sought to identify significant biological processes; estimates of minimum survival were less important than the model selection procedure. In searching for the simplest model that accounted for significant variation we considered rearing condition (PENRES, PEN60, PEN90, CAGE), gender (M,F), and year-site (Wyo., 1992; Wyo., 1993; S.D., 1994; Mont., 1994)). We then compared 2 strategies for model selection. The primary method involved selecting the most appropriate submodel on the basis of the lowest Akaike Information Criterion (AIC) value (Burnham et al., 1995). The second method was a reductionist approach, that started with the most complex general model and attempted to pool variables to arrive at a simpler model. In the latter method, we used likelihood ratio tests to compare nested submodels with more general models. Significant differences suggested the more complex model was needed. If several variables are nonsignificant, accepted convention favors first pooling the levels of the variable with largest probability of Type I error (Lebreton et al. 1992). When interpreting individual comparisons of models, results were judged significant if the probability of committing a Type I error was ≤ 0.05. The pooling that

occurs during model selection is a result of failure to reject the null hypothesis of no difference between models and should not be interpreted to mean there is no effect. Failure to reject can be due to inefficient experimental design, high variation, small samples, confounded variables, and other factors that have little to do with actual influence of treatments (Lebreton et al. 1992). Bracketing estimates that parenthetically follow a point estimate are symmetrical 95% confidence intervals based on simple binomial variation.

For further evaluation of the sources of variation involved in the 3 levels of preconditioning, we conducted *Z*-tests to compare each level with the others, within years (Pollock et al. 1989). Significance of *Z*-tests was judged with Bonferonni-corrected alpha levels (selected level/no. of tests).

RESULTS

Comparison of PENRES and CAGE Animals

For the short-term return data, the model selected via AIC (no. 6; Table 5.2) pooled genders and year-sites, which implies a significant effect of rearing (Fig. 5.1). With a sequence of likelihood ratio tests, genders were pooled first because the difference between the pooled-genders reduced model 5 (Table 5.2) and the general model (no. 1) was the least significant ($P = 0.289$) of the 3 comparisons. Next, we pooled year-site data were because model 6 did not differ from model 5 ($P = 0.226$). Model 7, however, differed from model 2 $P = 0.003$), so we retained the more complex model 7, which had separate return rate estimates for CAGE and PENRES animals.

For the long-term return data (Table 5.3), the conclusion from AIC was to pool only genders (no. 5), while likelihood ratio tests led to selection of the model pooling genders and year-sites (no. 6). Regardless of which model is most appropriate, the effect of rearing method remained significant (Fig. 5.2).

Comparison of PENRES, PEN60 and PEN90 Animals

Both AIC and the reduction process with likelihood ratio tests resulted in selection of model 5 (Table 5.4), which retained rearing categories and years (Fig. 5.3). Genders were pooled first, but year effect ($P = 0.010$) and rearing effect ($P = 0.046$) were significant. The Z-tests conducted on the 1995 Montana data (where sample sizes were best) hinted that the significant difference between the 3 levels of conditioning was mostly attributable to the difference between PENRES and PEN90 animals ($Z = 2.17$, $P = 0.038$), but no pairwise comparisons were significant when judged against the Bonferroni-adjusted alpha level (0.05/3 = 0.017).

Comparison of Males and Females

Overall, the mean return rate for males in 1992-94 (analysis summarized in Table 5.2) was 0.150 (±0.064), which was similar to the 0.189 (±0.089) rate for females. In the additional analysis of cage-reared animals in 1991-94 (Table 5.5), the return rate for males was 0.127 (±0.060), which was not different ($P = 0.544$) from females (0.139±0.080). Gender effect remained nonsignificant ($P = 0.107$) for the postwhelping surveys (about 9 months postrelease), but return rates had diverged to 0.043 (±0.042) for males and 0.109 (±0.082) females.

DISCUSSION

The pattern of differences between short-term return rates for PENRES and CAGE is consistent for most year-site combinations (Fig. 5.1). Rates for year-site categories appear different, but were not significant. Thus, the combined year-site depiction (Fig. 5.1) reflects appropriate estimates for these rearing groups. The combined site analysis of short-term return rates suggests a 2.7-fold difference between minimum survival of PENRES and CAGE, and the sparse long-term return data suggest more than a 10-fold difference (Fig. 5.2).

An assumption of equal detectability and trapability of treatment groups is necessary to make interpretations regarding comparative survival among treatments. Although we had little objective data on detectability, radiotagged CAGE ferrets were significantly more active aboveground than PENRES ferrets (Biggins et al., unpubl. data). If detectability is positively correlated with activity level, CAGE animals may have been more detectable than PENRES animals, and potentially caused underestimation of the difference between the 2 groups.

Several other assumptions are involved in making inferences from mark-recapture studies (Brownie et al. 1985). In this study, the population consisted of all animals released. Because every member of the population was marked, the assumption of representativeness of the sample was trivial, wherein we assumed we were dealing with true samples in the statistical sense.

Assuming independence of fates of individual animals was somewhat problematic because ferrets were reared as litters and often released as sibling pairs, which allowed

genetics, environment, and spatial associations to decrease differences between siblings compared to nonsiblings. Sibling correlation should not have biased our parameter estimates but could have caused variances to be underestimated. Because the number of litters in this study was large (n=113), we doubt sibling correlation led to inappropriate conclusions.

Tag loss would reduce estimates of minimum survival but should bias model selection only if rates of loss differed between treatment groups. We assumed an equal and low loss rate for all groups because few unmarked animals were captured.

The generally earlier spotlight surveys done in Wyoming would tend to increase return rate estimates. Those potentially inflated estimates should not greatly affect comparisons between rearing groups or genders, but failure to detect differences between sites in several of the selected models (Tables 5.2, 5.3, and 5.5) could have been influenced by these procedural differences. Questions regarding the influence of site on survival of ferrets remain largely unanswered.

The type of experience ferret kits received seems to have affected survival. The PENRES kits were in pens at an earlier age and were in pens longer than PEN90 kits; the PEN60 kits were intermediate in both respects. Thus, the pattern of relatively high survival of PENRES kits, low survival of PEN90 kits, and intermediate survival of PEN60 kits (Fig. 5.3) was intuitively appealing. The overall comparison of preconditioning strategies raises other questions regarding which of the several concurrent changes in environment had the greatest influence (e.g., presence of the dam in the PENRES and PEN60 groups, duration of the experience, age of kits when transferred to pens).

Because rearing effect was important in the model with 3 preconditioning levels, and PEN90 kits had lowest survival of the 3 levels, their skills possibly differed little from naive CAGE animals, but a test was not conducted. That comparison would have wide-reaching management implications, because many ferrets used in reintroductions are produced by zoos where outdoor pens are unavailable, and kits <90 days old usually are not transferred to conditioning facilities without their dams.

Animals that habitually are aboveground or make long aboveground movements may be most vulnerable to predation, which has been the cause of most mortality to released ferrets. An association between movements and survival is supported by behavioral analyses of radio-tagged ferrets (Biggins et al., unpubl. data) that show highest aboveground activity levels by CAGE ferrets and lowest activity by PENRES animals. Similarly, males in the free-ranging Meeteetse population moved more than females (Biggins et al. 1985), had larger areas of activity (K. Fagerstone and D. Biggins, unpubl. data), and must have had a higher mortality or dispersal rates than females because sex ratios are equal at birth (Williams et al. 1991) but were skewed toward females as adults (Forrest et al. 1988). Also, our failure to detect mortality differences between males and females at 1 month postrelease was accompanied by a failure to detect differences between genders in postrelease movements (Biggins et al., unpubl. data).

Failure to detect survival differences between males and females may mean the effect of gender is not dramatic at about 1 month postrelease, and any predisposition for differences may be overwhelmed by the presumably disruptive release process. The

longer-term return rates for released ferrets show the expected trend toward lower male survival, but the paucity of data prevents validation.

Confounding of important variables hinders interpretation of the increase in short-term ferret survival in Montana from 1994 to 1995. In 1995, postrelease support actions for ferrets (providing supplemental food and shelter) were eliminated, habitat quality (burrow density) was higher, electric fencing was added to exclude coyotes from release areas, and more coyotes were shot from aircraft. The individual effect of each of these changes remains speculative, and their combined effect on long-term survival is unknown.

Prairie dog density decreased about 32% at the Wyoming site between summer 1992 and summer 1993, and plague was suggested as a possible cause (B. Luce and R. Steiner, Wyo. Game and Fish Department Ann. Completion Rep., Cheyenne, Wyo., 1994). An additional decline of about 31% occurred on the core area sampled in 1994 (G. Staley and B. Luce, Wyo. Game and Fish Department 1994 Ann. Completion Rep., Cheyenne, Wyo., 1995).

Plague can kill black-footed ferrets (Williams et al. 1994). Hence, if the low return rate for ferrets released in fall 1993 (Fig. 5.1) was plague-related, early ferret mortality from plague could have nullified any developing differences between rearing groups because diseases probably would affect all animals indiscriminately. Lower return rates in 1994, coupled with evidence of persistent plague, resulted in cancellation of ferret releases for 1995 in Shirley Basin, Wyoming.

Estimated minimum survival rates for reintroduced black-footed ferrets were similar to the 12-15% survival of another small carnivore, the swift fox (*Vulpes velox*),

which was released onto Canadian prairies (Ginsberg 1994). Comparing survival of reintroduced ferrets to other ferret populations of more natural origin, however, may be more informative. The minimum 9-month survival rate of fully pen-experienced ferrets released onto the best habitat (>40%) was encouraging compared to the 37-41% annual survival rate for adult ferrets and 11% rate for kits in the Meeteetse population of wild ferrets (Forrest et al. 1988). Before reintroduction of black-footed ferrets began, general expectations were for survival rates to be lower than the Meeteetse rates when releasing relatively naive, captive-reared animals. In some cases, however, released ferrets have had several potentially compensating advantages over their wild ancestors: (1) some release sites had prey density several times greater than the prey density at Meeteetse, (2) ferrets released into ferret-unoccupied habitat may face less intraspecific competition, and (3) coyote management programs at some release sites may have reduced interspecific competition for prairie dogs as food and coyote predation on ferrets.

MANAGEMENT IMPLICATIONS

Pen-rearing provided demonstrated benefits, but efficiency possibly can be improved with other strategies. Further research is needed to assess the relative contributions of various environmental changes accompanying outdoor pen conditioning. For example, what size pen is adequate, and how much exposure to costly live prairie dogs is necessary? Holding and breeding ferrets entirely in outdoor pens is another option that may have reproductive benefits and may promote general health and welfare of ferrets. Conditioning of transients should be tested in pens located at reintroduction sites

(ours were at breeding facilities). Animals may become better acclimated to the local site and would not be stressed from long-distance shipment immediately before release.

We recommend use of outdoor pens for routine prerelease conditioning of black-footed ferret kits and suggest a cost-benefit analysis to explore feasibility of expanding their use at ferret production facilities and reintroduction sites. Use of outdoor pens should substantially enhance the rate of establishment of wild populations. Conversely, slow progress in the recovery program will tend to (1) result in higher long-term costs by delaying completion dates; (2) try the patience of cooperators, reducing political and financial support; and (3) increase the number of generations ferrets spend in captivity. The latter has several possible negative biological consequences resulting from genetic "bottleneck" effect, behavioral changes due to modified cultural adaptations to an artificial environment, and lack of natural selection.

LITERATURE CITED

Biggins, D. E., and M. H. Schroeder. 1988. Historical and present status of the black-footed ferret. Pages 93-97 *in* D. W. Uresk, G. L. Schenbeck and R. Cefkin, technical coordinators. Proceedings of the eighth Great Plains wildlife damage control workshop. U.S. Forest Service General Technical Report RM-154.

_____, _____, S. Forrest, and L. Richardson. 1985. Movements and habitat relationships of radio-tagged black-footed ferrets. Pages 11.1-11.17 *in* S. H. Anderson and D. B. Inkley, editors. Proceedings of the black-footed ferret workshop. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

_____, _____, _____, and _____. 1986. Activity of radio-tagged black-footed ferrets. Great Basin Naturalist Memoirs 8:135-140.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data--a handbook (second edition). U.S. Fish and Wildlife Service Resource Publication 156.

Burnham, K. P., G. C. White, and D. R. Anderson. 1995. Model selection strategy in the analysis of capture-recapture data. Biometrics 51:888-898.

Campbell, T. M. III, D. E. Biggins, S. C. Forrest, and T. W. Clark. 1985. Spotlighting as a method to locate and study black-footed ferrets. Pages 24.1-24.7 *in* S. H. Anderson and D. B. Inkley, editors. Proceedings of the black-footed ferret workshop. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Carpenter, J. W. 1984. Captive breeding and management of black-footed ferrets. Pages 12.1-12.13 *in* S. H. Anderson and D. B. Inkley, editors. Proceedings of the black-footed ferret workshop. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Clark, T. W., T. M. Campbell III, M. H. Schroeder, and L. Richardson. 1983. Handbook of methods for locating black-footed ferrets. Wyoming Bureau of Land Management Technical Bulletin 1.

Clark, M. M., and B. G. Galef. 1977. The role of the physical rearing environment of the Mongolian gerbil (*Meriones unguiculatus*). Animal Behaviour 25:298-316.

Fagerstone, K. A., D. E. Biggins, and T. M. Campbell III. 1985. Marking and radio-tagging of black-footed ferrets (*Mustela nigripes*). Pages 10.1-10.10 *in* S. H. Anderson and D. B. Inkley, editors. Proceedings of the black-footed ferret workshop. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

_____, and B. E. Johns. 1987. Transponders as permanent identification markers for domestic ferrets, black-footed ferrets, and other wildlife. Journal of Wildlife Management 51:294-297.

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

Ginsberg, J. R. 1994. Captive breeding, reintroduction, and the conservation of canids. Pages 365-383 *in* P. Olney, G. Mace, and A. Feistner, editors. Creative conservation: interactive management of wild and captive animals. Chapman and Hall, London, United Kingdom.

Greenough, W. T., and J. M. Juraska. 1979. Experience induced changes in brain fine structure: Their behavioral implications. Pages 263-294 *in* M.E. Hahn, C. Jensen, and B.C. Dudek, editors. Development and evolution of brain size: behavioral implications. Academic Press, New York, USA.

Huck, U. W., and E. O. Price. 1975. Differential effects of environmental enrichment on the open-field behavior of wild and domestic norway rats. Journal of Comparative Physiological Psychology 89:892-898.

Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs 36:239-273.

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.

Miller, B., D. Biggins, L. Hanebury, and A. Vargas. 1994. Reintroduction of the black-footed ferret (*Mustela nigripes*). Pages 455-464 *in* P. Olney, G. Mace, and A. Feistner, editors. Creative conservation: interactive management of wild and captive animals. Chapman and Hall, London, United Kingdom.

_____, _____, C. Wemmer, R. Powell, L. Calvo, L. Hanebury, and T. Wharton. 1990. Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*) II: predator avoidance. Journal of Ethology 8:95-104.

_____, R. Reading, and S. Forrest. 1996. Prairie night--black-footed ferrets and the recovery of endangered species. Smithsonian Press, Washington, D.C., USA.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 55:7-15.

Renner, M. J. 1988. Learning during exploration: the role of behavioral topography during exploration in determining subsequent adaptive behavior. International Journal of Comparative Psychology 2:43-56.

Richardson, L., T. W. Clark, S. C. Forrest, and T. M. Campbell III. 1987. Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming. American Midland Naturalist 117:225-239.

Rosenzweig, M. R. 1979. Responsiveness of brain size to individual experience: behavioral and evolutionary implications. Pages 263-294 *in* M.E. Hahn, C. Jensen, and B.C. Dudek, editors. Development and evolution of brain size: behavioral implications. Academic Press, New York, New York, USA.

Scott, J. P., and J. L. Fuller. 1965. Genetics and the social behavior of the dog. University of Chicago Press, Chicago, Illinois, USA.

Thorne, E. T., M. H. Schroeder, S. C. Forrest, T. M. Campbell III, L. Richardson, D. E. Biggins, L. R. Hanebury, D. Belitsky, and E. S. Williams. 1985. Capture, immobilization and care of black-footed ferrets for research. Pages 9.1-9.8 *in* S. H. Anderson and D. B. Inkley, editors. Proceedings of the black-footed ferret workshop. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

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

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

_____, E. T. Thorne, M. J. G. Appel, and D. W. Belitsky. 1988. Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming. Journal of Wildlife Diseases 24:385-398.

_____, _____, D. R. Kwiatkowski, S. L. Anderson, and K. Lutz. 1991. Reproductive biology and management of captive black-footed ferrets (*Mustela nigripes*). Zoo Biology 10:383-398.

White, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. Journal of Wildlife Management 47:716-728.

Table 5.1. Black-footed ferret releases used for assessment of effect of year-site, rearing condition, and gender on minimum survival (parentheses enclose number of ferrets released in each year-site).

Treatment[a]	1991	1992	1993	1994	1995	Total
CAGE	[b]Wyo. (49)	Wyo. (71)	Wyo. (35)	[c]Mont. (16) [d]S.D. (16)		187
PENRES		Wyo. (18)	Wyo. (13)	Mont. (9) S.D. (13)	Mont. (5)	58
PEN60				Mont. (7)	Mont. (17)	24
PEN90				Mont. (3)	Mont. (10)	13
Total	49	89	48	64	32	282

[a]CAGE = ferrets reared in traditional cages and released without experience in outdoor pens; PENRES = ferrets born in pens or born at facilities with pens and moved with dams to the pens when kits were <60 days old; PEN60 = ferrets transferred from a separate production facility to pens at a preconditioning facility (ca. 60-day-old kits were transferred with dams); PEN90 = ferrets transferred from a separate production facility to pens at a preconditioning facility (>90-day-old kits were transferred without dams).

[b]Shirley Basin, Wyoming.

[c]Charles M. Russell National Wildlife Refuge, Montana.

[d]Badlands National Park, South Dakota.

Table 5.2. Modeling short-term return rates of black-footed ferrets with 2 rearing groups (PENRES[a], CAGE[b]), genders, and 4 year-site combinations.

Model	$ln(L)$[c]	np[d]	AIC[e]	Vs. Model[f]	X^2	P
1 GENERAL	-16.286	16	64.573			
2 ALL SAME	-29.741	1	61.481	7	9.07	0.003
3 SITES SAME	-24.218	4	56.437	1	15.86	0.198
4 REARINGS SAME	-24.796	8	65.593	1	17.02	0.030
5 GENDERS SAME	-21.120	8	58.240	1	9.67	0.289
6 GENDER AND SITE SAME	-25.205	2	54.410	5	8.17	0.226
7 GENDER AND REARING SAME	-26.483	4	60.966	5	10.73	0.030
8 REARING AND SITE SAME	-29.489	2	62.977			

[a]PENRES = ferrets born in pens or born at facilities with pens and moved with dams to the pens when kits were <60 days old.

[b]CAGE = ferrets reared in traditional cages and released without experience in outdoor pens.

[c]*ln(L)* = log-likelihood.

[d]*np* = number of parameters.

[e]*AIC* = Akaike's Information Criterion.

[f]The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.

Table 5.3. Modeling long-term return rates of black-footed ferrets with 2 rearing groups (PENRES[a], CAGE[b]), genders, and 3 year-site combinations.

Model	$ln(L)$[c]	np[d]	AIC[e]	Vs. Model[f]	X^2	P
1 GENERAL	-5.863	12	35.725			
2 ALL SAME	-21.840	1	45.679	6	13.04	0.000
3 SITES SAME	-13.671	4	35.341	1	15.62	0.048
4 REARINGS SAME	-12.755	6	37.510	1	13.79	0.032
5 GENDERS SAME	-11.081	6	34.162	1	10.44	0.107
6 GENDER AND SITE SAME	-15.318	2	34.635	5	8.47	0.076
7 GENDER AND REARING SAME	-17.414	3	40.829	5	12.67	0.005
8 REARING AND SITE SAME	-20.742	2	45.485			

[a]PENRES = ferrets born in pens or born at facilities with pens and moved with dams to the pens when kits were <60 days old.

[b]CAGE = ferrets reared in traditional cages and released without experience in outdoor pens.

[c]*ln(L)* = log-likelihood.

[d]*np* = number of parameters.

[e]*AIC* = Akaike's Information Criterion.

[f]The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.

Table 5.4. Modeling short-term return rates of black-footed ferrets in Montana with 3 rearing groups (PENRES[a], PEN60[b], PEN90[c]), genders, and 2 years.

Model	$ln(L)$[d]	np[e]	AIC[f]	Vs. Model[g]	X^2	P
1 GENERAL	-6.539	12	37.079			
2 ALL SAME	-16.855	1	35.711			
3 YEARS SAME	-12.949	6	37.897	1	12.82	0.046
4 REARINGS SAME	-13.599	4	35.198	1	14.12	0.079
5 GENDERS SAME	-10.207	6	32.414	1	7.34	0.291
6 GENDER AND YEAR SAME	-15.872	3	37.745	5	11.33	0.010
7 GENDER AND REARING SAME	-15.055	2	34.111	5	9.70	0.046
8 REARING AND YEAR SAME	-16.234	2	36.468			

[a]PENRES = ferrets born in pens or born at facilities with pens and moved with dams to the pens when kits were <60 days old.

[b]PEN60 = ferrets transferred from a separate production facility to pens at a preconditioning facility (ca. 60-day-old kits were transferred with dams).

[c]PEN90 = ferrets transferred from a separate production facility to pens at a preconditioning facility (>90-day-old kits were transferred without dams).

[d]*ln(L)* = log-likelihood.

[e]*np* = number of parameters.

[f]*AIC* = Akaike's Information Criterion.

[g]The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.

Table 5.5. Modeling short-term return rates of cage-reared black-footed ferrets with genders and 5 year-site combinations.

Model	$ln(L)$[a]	np[b]	AIC[c]	Vs. Model[d]	X^2	P
1 GENERAL	-12.251	10	44.502			
2 ALL SAME	-16.392	1	34.785			
3 SITES SAME	-16.366	2	36.731	1	8.23	0.412
4 GENDERS SAME	-14.269	5	38.537	1	4.04	0.544

[a]*ln(L)* = log-likelihood.

[b]*np* = number of parameters.

[c]*AIC* = Akaike's Information Criterion.

[d]The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.

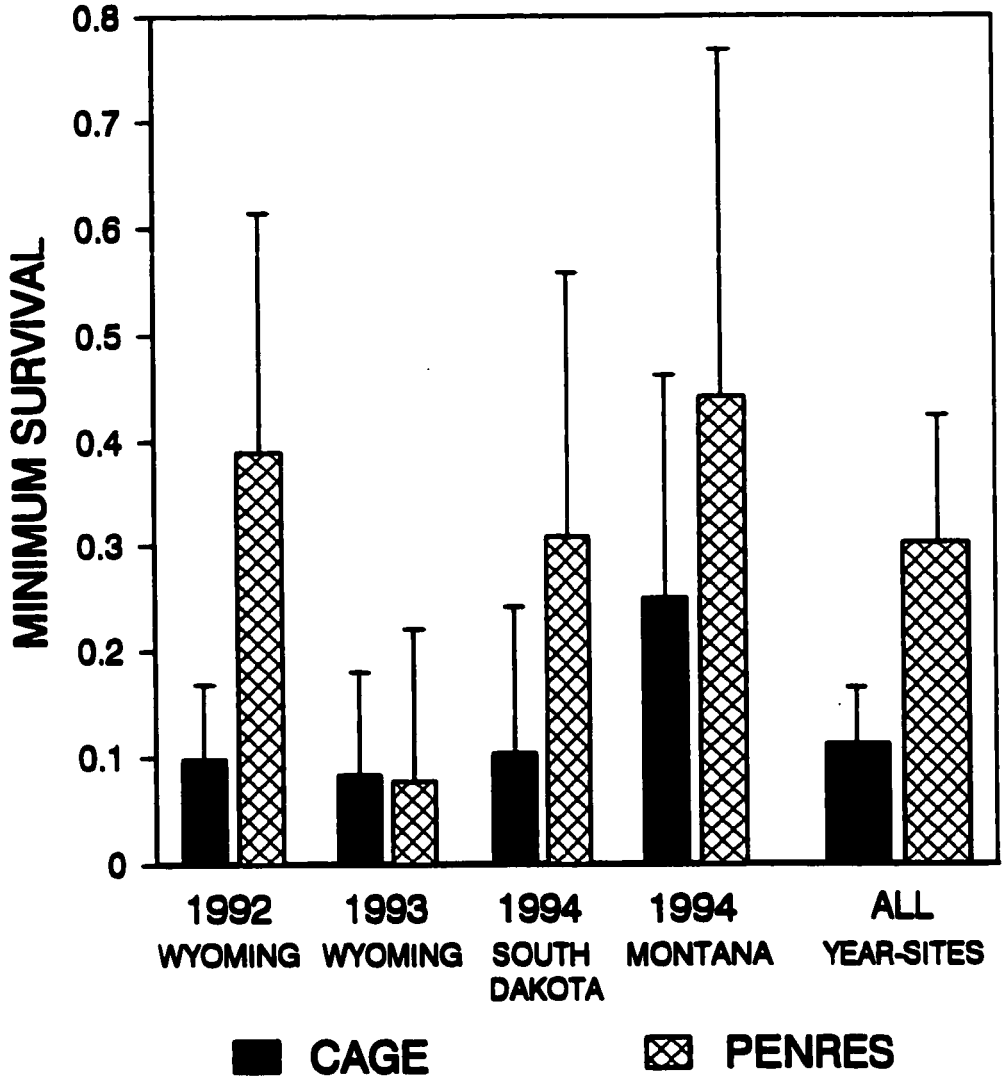

Figure 5.1. Minimum short-term (1 month) survival of young black-footed ferrets reared in cages and outdoor pens (means and upper bounds of 95% confidence intervals). Producers raised CAGE kits in traditional cages and we released them without experience in outdoor pens. The PENRES kits were born in pens or were born at facilities with pens and moved with dams to the pens when kits were <60 days old.

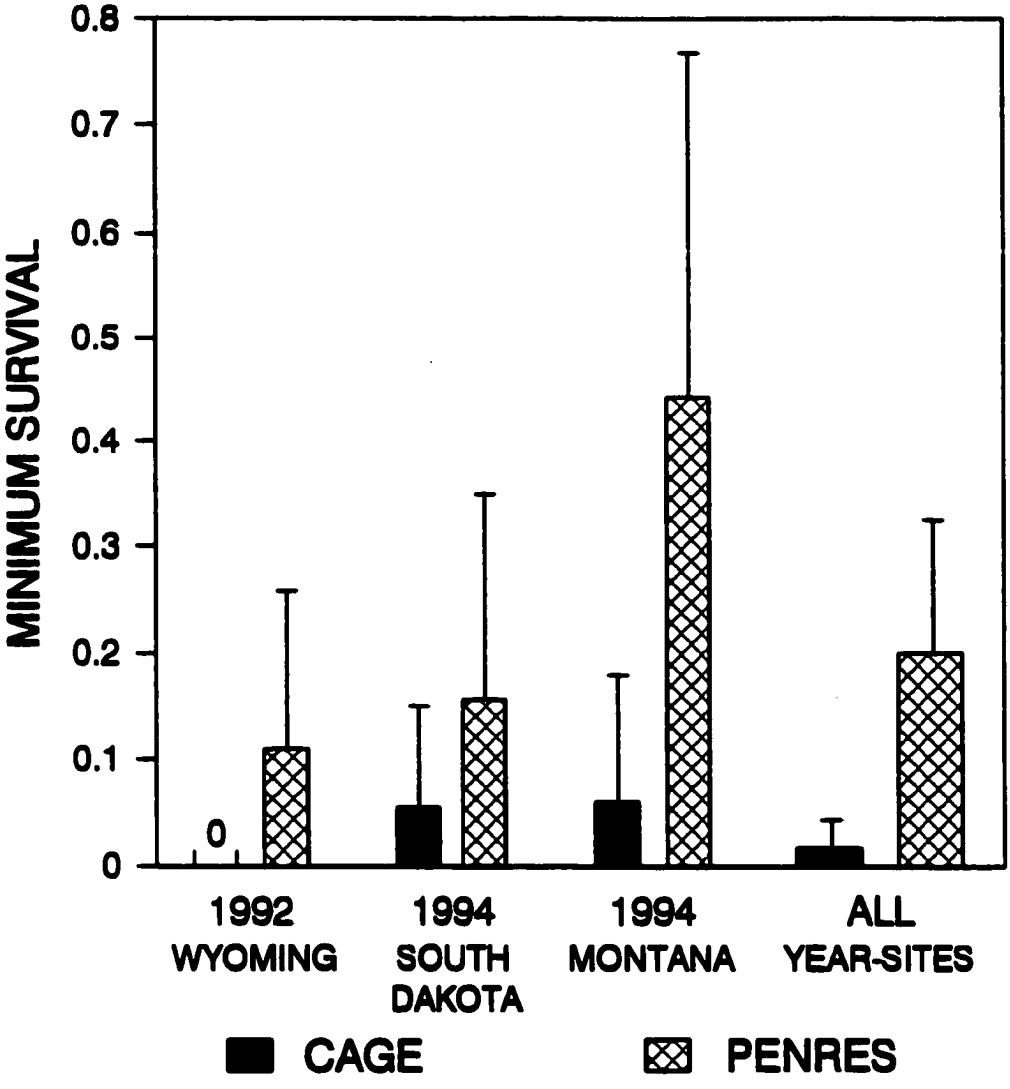

Figure 5.2. Minimum long-term (9 month) survival of young black-footed ferrets reared in cages and outdoor pens (means and upper bounds of 95% confidence intervals). Producers raised CAGE kits in traditional cages and we released them without experience in outdoor pens. The PENRES kits were born in pens or were born at facilities with pens and moved with dams to the pens when kits were <60 days old.

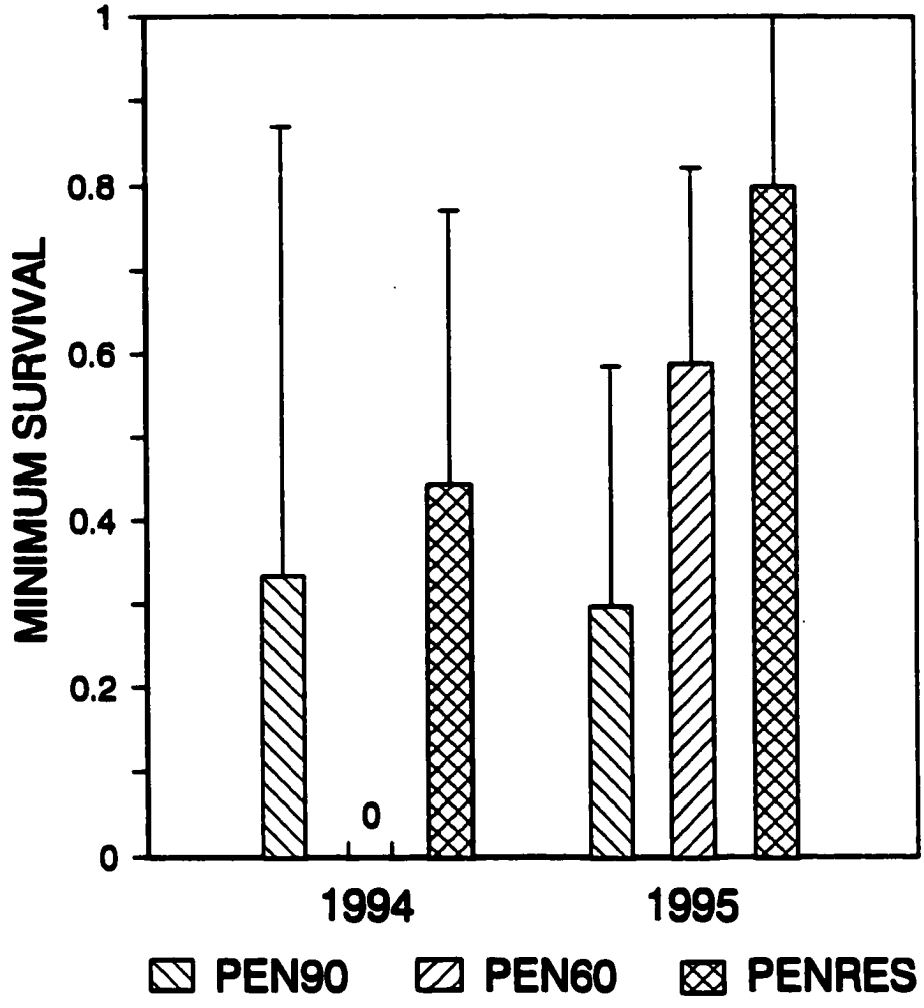

Figure 5.3. Minimum short-term (1 month) survival of young black-footed ferrets given 3 types of preconditioning experience in outdoor pens and released in Montana (means and upper bounds of 95% confidence intervals). The PENRES kits were born in pens or were born at facilities with pens and moved with dams to the pens when kits were <60 days old. We transferred PEN60 kits with dams from a separate production facility to pens at a preconditioning facility when kits were ca. 60 days old. We transferred PEN90 kits without dams from a separate production facility to pens at a preconditioning facility when kits were >90 days old.

CHAPTER 6

CONCLUDING REMARKS AND RECOMMENDATIONS

Predation Avoidance

Avoiding predation is critical to fitness (Lima and Dill, 1990); instead of being considered a constraint upon other issues of optimization, the other issues (e.g., energetic costs and benefits of different foraging strategies) may be considered the constraints on the central task of avoiding being killed. An organism can often miss a meal without long-term ill effect, but predation is final. For these and other reasons (Vermeij, 1994), one might expect "that most evolutionary change in predators is driven by their own predators or competitors not by their prey" (Brodie and Brodie, 1999).

Although musteline shapes and sizes are often explained in terms of foraging adaptations (King, 1990), the relative effects of selective forces related to hunting efficiency and predation avoidance that resulted in the slim bodies of mustelines cannot be disentangled. Their thin profiles and modest sizes allow these predators to hide within the burrows of their prey, avoiding other predators that hunt those prey. Elongated bodies provide greater mass and strength for overcoming prey that inhabit burrows of the same diameter the predators occupy (hinting at parallel evolution in snakes and Mustela). It seems likely, therefore, that musteline body conformation is a compromise resulting from selective forces working in concert though foraging and predation. The introduction of

stoats (Mustela erminea) to New Zealand provides experimental evidence supporting the effect of predation on body size in mustelines. In some regions of the country, New Zealand stoats became the largest in the world within about 100 years, purportedly adapting to large prey (King, 1990). The paucity of predators in New Zealand, however, may have allowed stoats to broaden their hunting tactics. Under low risk of predation, the advantage of being smaller to increase availability of hiding places became nebulous, while being larger may have been adaptive by allowing a wider range of prey to be taken.

The black-tipped tails of black-footed ferrets (Mustela nigripes) and Siberian polecats (M. eversmannii) may be another adaptation to predation avoidance, similar to the black-tipped tails of some weasels which seem to direct the attention of birds of prey away from vital body parts and result in more failed attacks (Powell, 1982). Seasonal color shifts in pelage of weasels (Mustela spp.) probably are maintained by selective pressure from predation (King, 1990). The pelage of black-footed ferrets shows little seasonal change compared to the Siberian polecats we imported from northeastern China (M. e. dauricus). The latter changed from a relatively dark reddish brown animal in summer to a much lighter buff colored animal, with a head that is nearly white in some individuals, in winter. The differences between ferrets and polecats in length and color of fur may be influenced by differing foraging tactics; increased aboveground hunting by polecats may have led to advantages in lighter colored and longer fur in winter. Although the steppe ranges of ferrets and polecats receive snow in winter, snow cover is probably less persistent than in the ranges of weasels (Mustela spp.) that have white winter pelage, leading to a less pronounced advantage of a pure white fur for polecats.

The scent glands of some mustelids are another morphological adaptation to predation avoidance (Wade-Smith and Verts, 1982). Two reintroduced black-footed ferrets were injured in apparent predator attacks but escaped immediate death, and coyotes (Canis latrans) commonly failed to consume ferrets and polecats they killed. The musk of ferrets and polecats seemed to have little value, however, in deterring avian predators or American badgers (Taxidea taxus), which consumed the ferrets and polecats they killed during our studies. The distinctive odors of polecats and ferrets may increase their detectability by mammalian predators. Overall, it seems more likely that the scent glands in mustelines evolved for intra- and inter-specific communication (e.g., individual and sexual recognition, territoriality) than for predation avoidance (Brinck et al. 1983; Erlinge and Sandell 1988).

Generalist and Specialist

Although black-footed ferrets and Siberian polecats have been termed "ecological equivalents" (Hoffmann and Pattie, 1968, p. 57), differences in life histories have been noted (Forrest et al., 1985) and studies detailed in chapters 2-4 suggested behavioral differences. Evolution of these behavioral attributes may have been influenced by predation. Compared to Siberian polecats, black-footed ferrets tend (1) to be predisposed to a diel activity cycle consistent with predator avoidance, (2) to rely less on risk assessment in decisions regarding activity, (3) to be prey specialists, and (4) to have smaller litters. The degree of prey specialization in black-footed ferrets, and prey generalization in Siberian polecats, may be, in part, responsible for the differences in evolution of predator avoidance behaviors (Chaps. 2, 4), but what differences in selective

pressure on the steppes of the two continents led to the differences in specialization and in potential productivity? Four hypotheses discussed below provide explanations (but are not intended to be exhaustive or mutually exclusive).

Hypothesis 1, Spatial Variation-- Generalization in polecats is due to region-wide (spatial) variation in availability of varied prey species. Specialization is a disadvantage, because it limits biomass of available prey. Over the large geographic range of Siberian polecats, there are varied ecological settings with many different species of grassland rodents and lagomorphs; the situation appears more varied than in North America. Lack of reproductive isolation thus results in polyphenetic generalist polecats with regionally adapted phenotypes (Slatkin, 1987), treated as subspecies by some taxonomists.

Hypothesis 2, Temporal Variation-- Temporal variation in prey abundance on Asian steppes (Elton, 1925) favors generalists (Wilson and Yoshimura, 1994). Prey switching is advantageous as various prey alternate in abundance, assuming somewhat asynchronous cycles of different prey. Further, specialization on a single type of prey may lead to extinction of the predator, at least locally, as those prey become rare. Plague (Yersinia pestis) leads to oscillations in populations of susliks (Spermophilus spp.), great gerbils (Rhombomys opimus), and other rodents of central Asia (Fig. 6.1), and polecat populations may be affected dramatically by these changes in prey numbers (Chelnokov et al., 1979; Gorbunov, 1983). The few polecats remaining after an epizootic of plague may be forced to shift to less preferred prey, similar to shifts in prey use that occur seasonally in some areas (Stroganov, 1962). In contrast, the historical lack of plague in North America (Barnes, 1993) may have allowed greater stability in populations of ground-

dwelling sciurids (Fig. 6.1), promoting specialization by ferrets on the most suitable forms of prey, prairie dogs (Cynomys spp.).

Hypothesis 3, Intraguild Predation-- Differences in intraguild predation in different habitats preclude use of some prey (and their habitats) that might otherwise be suitable. In North America, certain predators, for example great horned owls (Bubo virginianus) or coyotes may be more effective in preying on black-footed ferrets than are any of their Asian counterparts in preying on polecats. Ferret specialization on prey that provided high densities of burrows as escape cover may have been highly adaptive.

Hypothesis 4, Interspecific Competition-- Interspecific competition (other than direct interference competition) is a greater constraint on expansion of black-footed ferrets to other prey than it is for polecats in Asia. Within North American grasslands, other mustelines the size of ferrets are absent. Weasels (Mustela spp.) occur sympatrically with ferrets and polecats on both continents, but are smaller than ferrets and polecats. In Asia, marbled polecats (Vormela peregusna), mustelines only slightly smaller than Siberian polecats (Wilson and Reeder, 1993) and sympatric with them in many areas, may be locally abundant only when Siberian polecats are absent (Chelnokov et al., 1979). The competition hypothesis does not seem to help explain the difference in specialization of Asian and North American polecats.

The terms generalist and specialist are meaningful only in a comparative sense (Futuyma and Moreno, 1988), and the best explanation for specialization in black-footed ferrets compared to Siberian polecats may be a combination of the first three hypotheses. In this hybrid explanation, predation on ferrets and polecats (hypothesis 3) tends to

narrow their niches and promote specialization on both continents. In Asia, that influence is countered by the much larger and more diverse area of steppe and alpine meadow (spatial variation) serving as habitat for polecats, and by plague which causes large temporal variation in prey abundance. In North America, the selective pressure favoring specialization may have had no strong counter-force.

The restricted habitat of ferrets is likely to have been imposed by selective pressure from intraguild predation, perhaps primarily from coyotes. Ecological theory predicts that predation can be an important determinant of niche breadth (Ricklefs, 1990). The phenomenon of apparent competition centers on this issue (Holt, 1984), and there are numerous examples of species that have had spatial or temporal dimensions of their niches narrowed by predation in other ways (Gliwicz, 1986; Polis et al., 1989; Rydell and Speakman, 1995). Behaviorally, restricted use of habitats due to predation risk can occur on short time scales, where prey make choices based on sensory input (reviews in Lima and Dill, 1990), and over long time scales with behaviors becoming canalized (McIntosh and Townsend, 1994.). A more thorough review of the rodent and lagormorph species in North America compared to Asia might reveal why the niche of black-footed ferrets is narrow. It does not appear that other prey species create high densities of suitably-sized burrows for ferret refuges on the Great Plains, but two other western North American ground squirrels of size equal to Asian susliks (Spermophilus spp.) that are commonly prey for polecats are the Colombian ground squirrel (Spermophilus columbianus) and the California ground squirrel (S. beecheyi). Isolation may have prevented the range of California ground squirrels from being colonized by the ferrets. Colombian ground

squirrels are found near the range of the prairie dog, but are not known to have supported ferrets. Tests have not been conducted that would allow black-footed ferrets access to habitats with burrow densities and sizes similar to those of prairie dogs but created by other rodent species. Such studies might reveal whether black-footed ferrets are truly dependent on prairie dogs (as commonly stated), or are mainly influenced by the burrows of prairie dogs.

A purely contemporary consideration of adaptation and distribution of polecats and ferrets may be misleading. Organisms are honed continually by natural selection, but faunal assemblages also are influenced by past circumstances. Absences of some forms of life may be due to inability to recolonize after some perturbation made the former area temporarily unsuitable, the forms present are constrained by evolutionary history regarding the raw material on which selection can work (Gould, 1983), and random chance affects the process. Nevertheless, black-footed ferrets and Siberian polecats apparently coexisted in North America as recently as 30,000 years ago (Youngman, 1993, 1994), increasing the probability that either or both would have become modified to fill any additional roles that were suitable and available, either by generalizing, or diverging into additional specialized forms.

Yersinia pestis as a Predator

Plague results in high mortality rates in many species of mammals. Rather than exemplifying a co-evolved host-pathogen equilibrium (Mode ,1958), the plague bacillus Yersinia pestis acts more like a predator than do many other disease organisms. Siberian polecats evolved in the presence of plague, but plague apparently was not present in North

America (Barnes, 1993). Thus, comparison of polecats and ferrets might again be useful, asking whether any predation avoidance tactics analogous to those discussed above (endogenous activity patterns, risk assessment and active avoidance, post-contact defenses) could serve to reduce risk from plague. Ferrets and polecats are both highly susceptible to plague (Castle et al., 1999; Williams et al., 1994; Williams et al., 1996), as are most species of their prey. Because post-contact defense mechanisms (in this case immune response) seem relatively ineffective, avoidance seems to be the only solution. Assessment of risk by detecting the organism does not appear likely because neither polecats nor ferrets avoided plague-killed rodents (Biggins, unpublished data; Castle et al., 1999; Williams et al., 1996); both suffered high rates of mortality when they consumed plague-infected carcasses. Avoidance of carrion in general might reduce risk (although rodent fleas transmit the disease), but both polecats and ferrets readily consume dead animals (Biggins, unpublished data; Sviridenko, 1935). Plague seems to cause dramatic reductions in populations of polecats and their prey, implying lack of direct defense mechanisms. Indirectly, however, the life history of Siberian polecats may reflect the influence of plague.

Plague, Fluctuating Prey Populations, and r-K Selection

As emphasized by Ricklefs (1990, p. 578), "The importance of r-and-K selection theory, relative to other sources of variation in life histories, depends on demonstrating a direct link between differences in population fluctuations and life history traits in pairs of otherwise similar organisms." If Siberian polecats evolved in a more variable environment due in part to the presence of plague, and black-footed ferrets evolved in a relatively stable

environment, these closely related Mustela provide an opportunity to contrast the relative predictions of r-K selection theory (Calder, 1984; Eisenberg, 1983; Pianka, 1972). The prediction of greater fecundity in the r-selected form seems met by the larger average litter size of Siberian polecats ($\bar{x}$ = 8.5; Stroganov, 1962), compared to black-footed ferrets ($\bar{x}$ = 3.4; Hillman, 1968). Cannibalism of captive-born young is common in both ferrets and polecats (Biggins, unpublished data; Sviridenko, 1935; Williams et al., 1991), but whether females kill the young or simply eat those that die usually cannot be determined. The cannibalism of young by female ferrets and polecats suggests a mechanism by which an energetic investment of gestation can be partially recovered if more young are born than the mothers can rear. When populations of primary prey are depressed (e.g, because of plague), cannibalism enables downward adjustment of litter size prior to the large energetic demands of lactation (Miller et al., 1996) and subsequent demands of hunting to feed a large litter; under more favorable conditions the female can maintain high production. In a stable environment, optimal litter size would be expected to be more constant, and greatest efficiency over the long term would be achieved by conceiving the number of young that could be reared consistently. The smaller litters of black-footed ferrets (compared to polecats) thus suggest the K-selected maximization of energetic efficiency.

Moreover, European mink (Mustela lutreola), European polecats (M. putorius), and Siberian weasels (M. sibirica), Eurasian congenerics similar to Siberian polecats in size, have smaller mean litter sizes than the latter (reviewed by Forrest et al., 1985), providing additional evidence supporting relative K-selection induced by a more stable

prey base. European mink and European polecats live mostly west of the Ural Mountains (Ognev, 1931), and therefore west of major plague foci in central Asia (Pollitzer and Meyer, 1961). Also, much of the diet of these mustelids consists of aquatic heterotherms (fish and amphibians), organisms unaffected by plague. The central Asian plague foci are coincident with much of the range of Siberian polecats and Siberian weasels, although the latter extends into the taiga. Siberian weasels prefer forested and riparian habitats, and are absent from open steppes (Bakeev, 1971). Siberian weasels kill a wide variety of small mammals, but little is known about the incidence of plague in their prey and in their forested habitats. Although many other environmental variables could have influenced the evolution of litter sizes in these species (Forrest et al., 1988), the outcome is generally consistent with an explanation of plague-induced instability in rodent populations, using both intra-Asian comparisons and Asian-North American comparisons.

Parenthetically, plague also may be responsible for the absence of an Asian social ground squirrel ecologically similar to the prairie dog. Coloniality enhances the hazard of disease transmission (with plague, the transmission by fleas and the possibility of transmitting the disease by direct contact). When plague is epizootic the costs of coloniality would be high, and selection should favor individuals with non-social tendencies. When plague is absent, kin selection could add to the benefits of a colonial social system (Hoogland, 1995). There is an oscillating target for natural selection as plague waxes and wanes; but in their plague-altered environment, the costs of the prairie dogs' social system may outweigh the benefits in the long term. Selective pressure from plague may ultimately transform prairie dogs into less social animals.

The removal of wolves (Canis lupus), a top predator of North American grasslands, combined with the addition of another major "predator" (plague) may have had synergistically deleterious effects on black-footed ferrets. The introduction of plague to North America, particularly, raises questions regarding habitat for black-footed ferrets (notwithstanding the high susceptibility of ferrets themselves to plague). Plague may have transformed North American steppes from black-footed ferret habitat into Siberian polecat habitat if temporal variation in prey abundance (hypothesis #2) is an important consideration. If intraguild predation (hypothesis #3), however, is influential enough to eliminate polecat use of habitats occupied by alternative prey (assuming polecats could adapt to prairie dogs as prey), the transformation resulting from plague may preclude potential occupancy of North American steppes by any polecat or ferret. Coyotes, the North American predators with greatest potential for restricting the ferrets' niche, are relatively resistant to Y. pestis (and may be more abundant due to wolf removal), and birds of prey are completely unaffected by direct exposure to Y. pestis. Furthermore, these predators are generalists that can minimize effects of plague-induced prey declines by switching between prey species.

Predator Avoidance Behaviors

An immediate cost of temporal avoidance of predators, whether considering genetically predisposed diel patterns of activity or decision-making based on risk assessment, is reduced opportunity to carry out other necessary activities related to foraging or reproduction (Lima, 1998). The cost/benefit considerations of canalized versus decision-based predator avoidance behaviors are similar to the cost/benefit comparisons of

foraging specialists and generalists (Bernays, 1998; Dall and Cuthill, 1997; Real, 1992). Compared to endogenous avoidance patterns, risk assessment and decision-making have the additional costs of (1) energetic investment attendant with any movement associated with risk assessment, (2) lost time and energy involved with increased exposure to adverse climates (compared to the burrow refugium), (3) increased exposure to predation during the sensory input stage, (4) energetic investments involved with neural processing of sensory information regarding risk and (5) the "overhead" costs of building and maintaining the neural and sensory architecture needed to conduct these activities. The last two costs may vary considerably depending on whether the response to sensory input is relatively fixed or varies by degree or even qualitatively depending on strength, type, and number of sensory inputs, and on learning (Real, 1992).

It does not seem essential, however, for a specialist such as the black-footed ferret to rely on canalized avoidance behaviors, and endogenous patterns, risk assessments, decision-making, and learning are not mutually exclusive. Black-footed ferrets and Siberian polecats demonstrate both canalized and context-dependent anti-predator behaviors, but in varying degrees. The best examples of fixed behaviors are the diel activity pattern of black-footed ferrets and the flight-to-burrow reaction to perceived direct threats (both species). There is a suggestion of risk assessment in the tendency of free-ranging black-footed ferrets to remain for varying spans of time (minutes to > 1 h) at the entrance of a burrow during its first emergence following a rest period (D. E. Biggins, unpublished data), and "alert" behavior has been described in detail (Clark et al., 1986; Miller and Anderson, 1993). In contrast to the Siberian polecats in our laboratory tests,

however, tested ferrets did not seem to alter exploration behavior after being challenged by a predator model. Although both species demonstrated predisposed nocturnality and positive response to moonlight, polecats seemed more influenced by the varying moonlight, and were less nocturnal. Estimates of predator-specific hazard rates for ferrets during different times of day and night, and data on activity patterns of ferret predators in the prairie dog ecosystem are needed to further evaluate our suggestion that predation pressure explains the diel activity preferences of black-footed ferrets. In general however, polecats seem to be more behaviorally flexible than ferrets.

The differing responses of polecats and ferrets to lighting suggests different selective pressures in their evolutionary history. In their native habitat, polecats (especially males) may be too large to hunt within the burrows of their prey (E.I. Denisov, pers. comm.). If hunting of rodents by polecats often occurs aboveground, then moonlight may be necessary to forage effectively. In black-footed ferrets, moonlight may be needed only for navigation, because ferrets kill in burrows where it would be dark regardless of surface conditions. The "eyeshine" of black-footed ferrets appears more intense than does the eyeshine of Siberian polecats when spotlights are used to locate these animals. Greater reflectance of the tapetum lucidum may be associated with increased scotopic capability in the ferrets, as compared to polecats, consistent with our results showing greater nocturnality in ferrets. Comparative study of eye morphology in these mustelids would be useful.

Black-footed ferrets and Siberian polecats do not seem to exemplify "ecological equivalence" defined as "The situation in which two or more species can replace each

other in the same ecological niche..." (Lincoln et al., 1998). A second definition, referring to "Unrelated or distantly related species fulfilling similar ecological roles in different communities..." (Lincoln et al., 1998) is equally inapplicable. These ferrets and polecats both inhabit grasslands in North America and Asia respectively, but they are closely (rather than distantly) related, and similarity of roles is debatable. Observations from the preceding chapters and other studies suggest that natural selection has resulted in considerable divergence of behaviors and non-skeletal features in these two extant forms of Mustela. This evidence weakens the contention that there should be a "broader range of possibilities for conservation of the black-footed ferret" (Owen et al., 2000), an argument based on similarities between black-footed ferrets and Siberian polecats and the hypothetical roles of North American Pleistocene and Holocene forms.

Generational Changes and Rearing Environments

The influence of rearing environment on survival of black-footed ferrets, coupled with the evidence regarding generational changes in behavior of captive Siberian polecats that seem to be heritable or culturally transmitted, seem contradictory. If such changes are progressive, and especially if they are heritable, they should not be reversible by rearing young for a few months in a natural setting. Nevertheless, we did not directly examine generational change in black-footed ferrets. Although the behaviors of fourth generation ferrets were similar to those of fourth generation polecats, behaviors of earlier generations of ferrets were not quantified. If behaviors of ferrets did not change, or changed less dramatically, the explanation could be relative lack of genetic variability, a critical ingredient for any type of selection. Second, the increased survival of ferrets due to

rearing does not necessarily suggest that the boldness behaviors we examined in the laboratory have reverted to "normal." Rearing in natural burrows may affect a larger suite of untested behaviors and interactions between them that result in altered predation risk to both bold and shy ferrets. We were able to demonstrate both rearing effects and generational changes in polecats. Consistent with the generally recognized false dichotomy of "nature vs. nurture" arguments (reviewed by Dawkins, 1986), the best explanation is that both are important and work in concert. This tenet does not negate the value of future research that might elucidate the relative importance of genetic change, cultural transmission, and environmental influences on development of behaviors in ferrets and polecats. It would be interesting, for example, to compare behaviors of cage-reared and pen-reared groups of fourth or fifth generation captive polecats using the owl trials of Chapter 2, or to use cross-fosterings of wild polecats and domestic ferrets to examine the relative effects of heredity and environment during rearing of these carnivores.

Regardless of the underlying cause, the 10-fold improvement in survival of released pen-reared black-footed ferrets compared to cage-reared ferrets was a turning point in the recovery program. The substantial financial savings were an immediate benefit, but continued sluggish progress in the project would likely have resulted in higher long-term costs by delaying completion dates, and would have tested the patience of cooperators, jeopardizing future political and financial support. Biological costs of low survivorship include greater loss of genetic diversity due to slower expansion of the ferret population, genetic change due to lack of natural selection and unintentional artificial selection, and additional behavioral changes due to cultural adaptation to an artificial

environment. Perhaps the most important management recommendation stemming from this research, therefore, is to rear black-footed ferrets in a quasi-natural environment from the earliest age practical, especially those animals to be released in the wild. Also, the maintenance of captive breeding stock in such environments may delay behavioral changes such as those noted during the four generations of cage-rearing of Siberian polecats.

LITERATURE CITED

Bakeev, Yu. N. 1971. The distribution and population dynamics of the Siberian kolinsky in the western part of its range in the USSR. Pp. 149-159 in King, C. M. (ed.), Biology of Mustelids, Some Soviet Research, Volume 2. New Zealand Department of Scientific and Industrial Research Bulletin 227, Wellington.

Barnes, A. M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pp. 28-37 in J.L. Oldemeyer, D.E. Biggins, and B.J. Miller, eds., Management of Prairie Dog Complexes for the Reintroduction of the Black-footed Ferret, Biological Report 93-13, U.S. Fish and Wildlife Service, Wash. D.C.

Bernays, E. A. 1998. The value of being a resource specialist: behavioral support for a neural hypothesis. American Naturalist 151:451-464.

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.

Brinck, C., S. Erlinge, and M. Sandell. 1983. Anal sac secretion in mustelids. A comparison. Journal of Chemical Ecology 9:727-746.

Brodie, E. D., III., and E. D. Brodie, Jr. 1999. Predator-prey arms races. Bioscience 49:557-568.

Calder, W. A., III. 1984. Size, function, and life history. Harvard University Press. London.

Castle, K., D. Biggins, L. Carter, K. Innes, M. Chu, and J. Wimsatt. 1999. Susceptibility of the Siberian polecat (Mustela eversmannii daurica) to subcutaneous and oral plague (Yersinia pestis) exposure. Unpublished report, USGS/BRD, Midcontinent Ecological Science Center, Fort Collins, Colorado.

Clark, T. W., L. Richardson, S. C. Forrest, D. E. Casey, and T. M. Campbell III. 1986. Descriptive ethology and activity patterns of black-footed ferrets. Great Basin Naturalist Memoirs 8:115-134.

Chelnokov, V. N., A. Zuichenko, and Yu. Fedyashev. 1979. Fluctuations of the southern boundary of the range of the steppe polecat in western Turkmenia. Moskovskoe Obshchestvo Ispytatele i Prirody, Biulleten, 84:46-48.

Dall, S. R. X., and I. C. Cuthill. 1997. The information costs of generalism. Oikos 80:197-202.

Dawkins, M. S. 1986. Unraveling animal behaviour. Longman Group, Ltd. U.K.

Elton, C. S. 1925. Plague and the regulation of numbers in wild mammals. The Journal of Hygiene 24:138-163.

Eisenberg, J. F. 1981. The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. Univ. of Chicago Press, Chicago, Illinois.

Erlinge, S., and M. Sandell. 1988. Coexistence of stoat, Mustela erminea, and weasel, M. nivalis: social dominance, scent communication, and reciprocal distribution. Oikos 53:242-246.

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

_____, T. W. Clark, L. Richardson, D. Biggins, K. Fagerstone, and T. M. Campbell III. 1985. Life history characteristics of the genus Mustela, with special reference to the black-footed ferret, Mustela nigripes. Pp. 23.1-11.14 in S. W. Anderson and D. B. Inkley (eds.), Black-footed Ferret Workshop Proceedings, Wyoming Game and Fish Department, Cheyenne.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology and Systematics 19:207-233.

Gliwicz, M. J. 1986. Predation and the evolution of vertical migration in zooplankton. Nature 320:746-748.

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

Gould, S. J. 1983. Hen's teeth and horse's toes: further reflections in natural history. W. W. Norton and Company, New York.

Hillman, C. N. 1968. Field observations of black-footed ferrets in South Dakota. Transactions of the North American Wildlife and Natural Resources Conference 33:433-443.

Hoffmann, R. S. and D. L. Pattie. 1968. A guide to Montana mammals. University of Montana, Missoula. 133 pp.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124:377-406.

Hoogland, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.

King, C. 1990. The natural history of weasels and stoats. Cornell University Press. Ithaca, New York. 253 pp.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48:25-34.

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. Cambridge University Press, Cambridge, United Kingdom.

McIntosh, A. R., and C. R. Townsend.1994. Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. Ecology, 75, 2078-2090.

Miller, B. J., and S. H. Anderson. 1993. Ethology of the endangered black-footed ferret (Mustela nigripes). Advances in Ethology 31: 1-46.

_____, R. P. Reading, and S. Forrest. 1996. Prairie night. Smithsonian Institution Press, Washington, D.C.

Mode, C. J. 1958. A mathematical model for the co-evolution of obligate parasites and their hosts. Evolution 12158-165.

Ognev, S. I. 1931. Mammals of eastern Europe and northern Asia, Carnivora, Fissipedia, Vol. II. Israel Program for Scientific Translations, Jerusalem.

Owen, P. R., C. J. Bell, and E. M. Mead. 2000. Fossils, diet, and conservation of black-footed ferrets (Mustela nigripes). Journal of Mammalogy 81:422-433.

Pianka, E. R. 1972. r and K selection or b and d selection. American Naturalist 106:581-588.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20:297-330.

Pollitzer, R., and K. F. Meyer. 1961. The ecology of plague. Pp. 433-590 in J. M. May (ed.), Studies in Disease Ecology. Hafner Publishing Company, Inc., New York.

Powell, R. A. 1982. Evolution of black-tipped tails in weasels: predator confusion. American Naturalist 119:126-131.

Real, L. A. 1992. Information processing and the evolutionary ecology of cognitive architecture. American Naturalist 140:S108-S145.

Ricklefs, R. E. 1990. Ecology. W.H. Freeman and Company, New York.

Rydell, J., and J. R. Speakman. 1995. Evolution of nocturnality in bats: Potential competitors and predators during their early history. Biological Journal of the Linnean Society 54:183-191.

Slatkin, M. 1987. Gene flow and the geographic sturcture of natural populations. Science 236:787-792.

Stroganov, S. U. 1962. Carnivorous Mammals of Siberia. Translation: Israel Program for Scientific Translations, Jerusalem, 1969. U.S. Dept. Commerce, Clearinghouse for Federal Scientific and Technical Information, Springfield, Virginia 22151.

Sviridenko, P. A. 1935. The steppe polecat (Putorius eversmanni) and its agricultural importance in the control of rodents. Izdatel'stvo VASKhNIL, Moskva-Leningrad. 151 p. (translation).

Vermeij, G. J. 1994. The evolutionary interaction among species: Selection, escalation, and coevolution. Annual Review of Ecology and Systematics 25:219-236.

Wade-Smith, J., and B. J. Verts.1982. Mephitis mephitis. Mammalian Species 173:1-7.

Williams, E. S., K. Mills, and A. Boerger-Fields. 1996. Plague in orally exposed black-footed ferret X Siberian polecat hybrids. Abstract in 45th Annual Conference of the Wildlife Disease Association, University of Alaska, Fairbanks.

_____, _____, D. R. Kwiatkowski, E. T. Thorne, and A. Boerger-Fields. 1994. Plague in a black-footed ferret (Mustela nigripes). Journal of Wildlife Disease 30:581-585.

_____, E. T. Thorne, D. R. Kwiatkowski, S. L. Anderson, and K. Lutz. 1991. Reproductive biology and management of captive black-footed ferrets (Mustela nigripes). Zoo Biology 10:383-398).

Wilson, D. E., and D. M. Reeder. 1992. Mammal species of the world: a taxonomic and geographic reference, second edition. Smithsonian Institution Press.

Wilson, D. S., and J. Yoshimura. 1994. On the coexistence of specialists and generalists. The American Naturalist 144:692-707.

Youngman, P. M. 1993. The Pleistocene small carnivores of eastern Beringia. The Canadian Field-Naturalist 107:139-163.

_____. 1994. Beringian ferrets: mummies, biogeography, and systematics. Journal of Mammalogy 75:454-461.

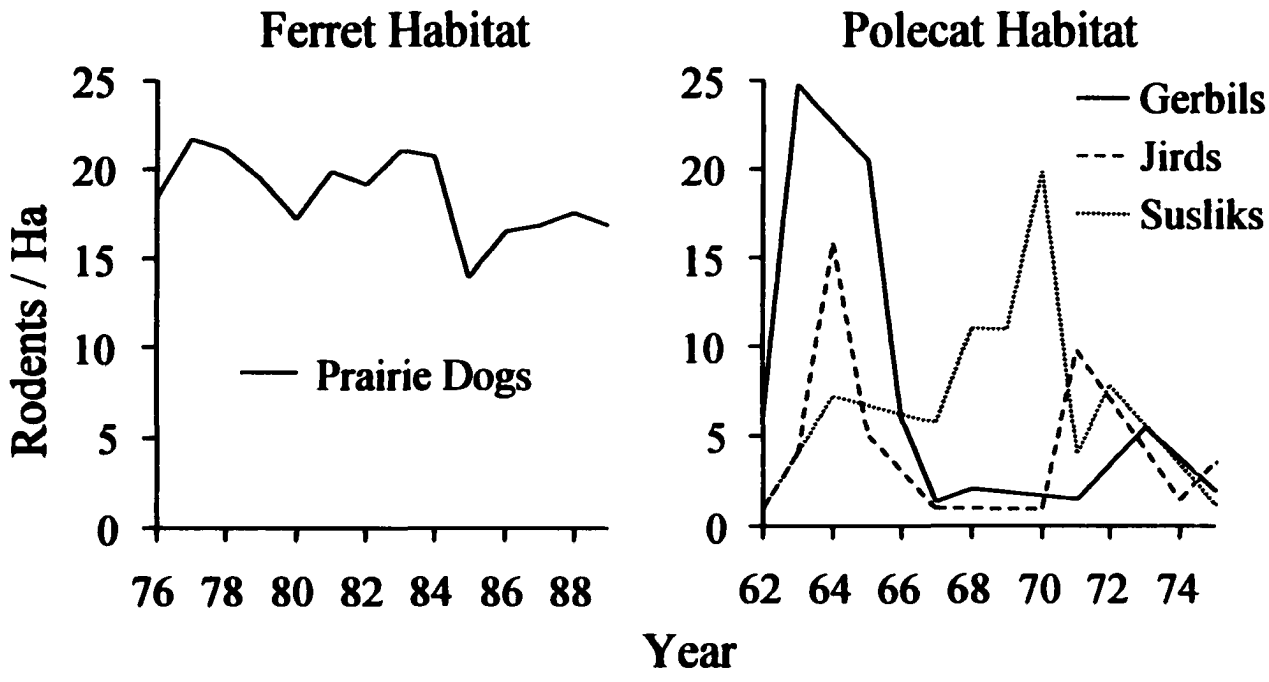

Figure 6.1. Fluctuations in densities of black-tailed prairie dogs (Cynomys ludovicianus) in North American habitat of black-footed ferrets and densities of great gerbils (Rhombomys opimus), Libyan jirds (Meriones libycus), and yellow susliks (Spermophilus fulvus) in Asian habitat of Siberian polecats. Data were extracted from Hoogland (1995) and Gorbunov (1983).