

U.S. Department of the Interior DIRK KEMPTHORNE, Secretary

U.S. Geological Survey

P. Patrick Leahy, Acting Director

U.S. Geological Survey, Reston, Virginia: 2006

For product and ordering information:

World Wide Web: http://www.usgs.gov/pubprod

Telephone: 1-888-ASK-USGS

For more information on the USGS--the Federal source for science about the Earth, its natural and living resources,

natural hazards, and the environment: World Wide Web: http://www.usgs.gov

Telephone: 1-888-ASK-USGS

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Although this report is in the public domain, permission must be secured from the individual copyright owners to reproduce any copyrighted materials contained within this report.

Suggested citation:

Roelle, J.E., Miller, B.J., Godbey, J.L., and Biggins, D.E., eds., 2006, Recovery of the black-footed ferret—progress and continuing challenges: U.S. Geological Survey Scientific Investigations Report 2005–5293, 288 p.

Does Predator Management Enhance Survival of Reintroduced Black-footed Ferrets?

By Stewart W. Breck, Dean E. Biggins, Travis M. Livieri, Marc R. Matchett, and Valerie Kopcso

Abstract

Predation on black-footed ferrets (Mustela nigripes) is a potential problem at reintroduction sites, causing up to 95 percent of the documented mortality of ferrets. Strategies to reduce mortality due to predation can focus on preconditioning ferrets prior to reintroduction and/or managing predators of ferrets. Biologists have tried three general strategies to control predators at reintroduction sites: (1) selective removal of individual predators, (2) nonselective removal of coyotes (Canis latrans), and (3) electric fences to exclude coyotes from release sites. We conducted a post hoc review of data from releases during 1994-2003 at 11 sites in South Dakota and Montana to address whether or not predator management has benefited reintroduced black-footed ferrets. Limited evidence indicates that (1) individual great horned owls (Bubo virginianus) can cause significant ferret mortality and that identifying and removing these individuals can be beneficial, (2) lethal control of coyotes may have inverse effects on ferret survival, and (3) electric fencing does not enhance short- or long-term survival of reintroduced ferrets. The data are confounded by a variety of factors, making conclusions tenuous. Well designed studies are needed to properly address the effectiveness of predator management for enhancing ferret survival.

Keywords: black-footed ferret, *Bubo virginianus*, *Canis latrans*, coyote, electric fencing, great horned owl, *Mustela nigripes*, predator control

Introduction

Successful recovery of black-footed ferrets (*Mustela nigripes*) will ultimately depend upon our ability to understand and manage a number of ecological factors (e.g., genetic inbreeding, disease, habitat, and predation) that influence survival, reproduction, and recruitment of ferrets in recovering populations. The role of predators in ecology, conservation biology, and wildlife management has gained increasing recognition as a factor to understand and potentially manage (Estes and others, 2001; Terborgh and others, 1999). For ferrets, mammalian and avian predation has been identified as a critical ecological component in both established populations (Forrest and others, 1988) and reintroduction efforts (Biggins and others, 1998; Biggins, 2000; Biggins, Godbey, Livieri, and others, this volume).

For example, at Meeteetse, Wyo., where the ancestral free-ranging population of ferrets was studied, 57 percent of known mortality of wild ferrets was due to predation (Forrest and others, 1988). Predation by great horned owls (Bubo virginianus), golden eagles (Aquila chryseatos), and coyotes (Canis latrans) was recorded, leading Forrest and others (1988) to conclude that in the Meeteetse ferret population: (1) annual mortality was high, (2) few if any ferrets lived to 3+ years, (3) 59 percent to 77 percent of all juveniles disappeared each year (when disease was not present), (4) adults disappeared at a rate about 80 percent of that seen in juveniles, and (5) predation was the most significant cause of ferret mortality (when disease was not present). For reintroduced animals, predation is equally if not more important, accounting for over 95 percent of the ferrets lost from reintroductions (Biggins, 2000; Biggins, Godbey, Livieri, and others, this volume). For those ferrets killed by predators, coyotes accounted for over 60 percent of the mortality and may have accounted for another 20–30 percent of unconfirmed predation. Badgers (*Taxidea* taxus), great horned owls, and other raptors accounted for a small portion of the predation.

A number of factors likely contribute to the dynamics of predator-ferret interactions, including predator density and behavior, availability of alternative prey, habitat conditions, and, for reintroduced animals, the level of preconditioning individuals receive before being released to the wild. Preconditioning enhanced survival of reintroduced ferrets and Sibe-

¹U.S. Department of Agriculture, National Wildlife Research Center, 4101 LaPorte Ave., Fort Collins, CO 80521.

²U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Ave., Bldg. C, Fort Collins, CO 80526.

³Prairie Wildlife Research, P.O. Box 515, Wall, SD 57790.

⁴U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, P.O. Box 110, Lewistown, MT 59457.

⁵U.S. Bureau of Land Management, Malta Field Office, HC 65, Box 5000, Malta, MT 59538.

rian polecats (Mustela eversmannii; Biggins and others, 1991, 1998, 1999). The foregoing research helped lead to establishment of a general preconditioning program for all ferrets released into the wild. Concurrent with the preconditioning research, biologists and managers from different release sites also tried techniques for managing predators to enhance survival of newly released ferrets. Early studies indicated that mortality of surrogate Siberian polecats was higher in areas with more predators (Biggins and others, 1991). Predator management primarily focused on coyotes and included both lethal and nonlethal techniques. Lethal management primarily involved removing coyotes in and around release areas prior to release of ferrets. To a lesser extent badgers and great horned owls were occasionally killed, mostly in attempts to stop individuals that apparently developed a search image for ferrets. In addition to lethal control, many release sites used electrified fencing to exclude terrestrial predators (primarily coyotes and badgers) for short periods (30-60 days postrelease). The results of these management actions have not been synthesized and published outside of internal reports. Our objective here is to explore existing data to determine if lethal coyote control, electric fencing, or selective removal of individual predators enhanced short-term and/or long-term survival of reintroduced black-footed ferrets.

Study Area and Methods

We synthesized data from black-footed ferret reintroduction sites in Montana and South Dakota and only used data on ferrets that had been preconditioned. Although other data were available from releases in Wyoming, Arizona, and Colorado/Utah, differences in prairie dog (*Cynomys*) species, preconditioning of ferrets, detectability of ferrets, and monitoring methodology from these sites precluded their inclusion in this analysis. In Montana a total of 10 releases occurred from 1994 to 2003, and in South Dakota, 10 releases occurred from 1994 to 1999 (table 1). All releases occurred on black-tailed prairie dog (*C. ludovicianus*) colonies, with higher densities of prairie dogs occurring on the South Dakota sites.

For each release, both short-term (30 days postrelease) and long-term (6–8 months postrelease) estimates of survival were determined by spotlighting ferrets (Campbell and others, 1985). Each survival estimate was based on a multiple night effort in which personnel in vehicles and on foot surveyed release areas with spotlights to detect ferrets. Any ferret detected was identified by using an automatic passive integrated transponder (PIT) reader placed at the burrow containing the animal (Biggins, Godbey, Matchett, and others, this volume). Transponders (i.e., PIT tags) were implanted subcutaneously in each individual prior to release. Survival rates were calculated as the percent of ferrets found alive and thus represent minimum survival estimates. Lack of replication in spotlight surveys over short time spans prevented separate

estimation of detection rates and survival rates, precluding the use of more sophisticated methods of survival analysis.

We used short- and long-term minimum survival estimates to evaluate whether lethal coyote control and/or electric fencing increased ferret survival. Lethal coyote control was carried out in a variety of ways and intensities across release sites and years. Some release sites were subjected to extensive coyote removal in and around release areas. At other sites smaller numbers of coyotes were removed in conjunction with disease monitoring, and at some sites no coyote removal was performed (table 1). We categorized the level of coyote control as high, medium, or low. High intensity control combined aerial gunning, opportunistic removal onsite, and disease sampling. Medium intensity control combined opportunistic removal onsite and disease sampling in and around the release area. Low intensity effort involved just disease sampling or no lethal control.

Electric fencing (ElectroNetTM; Premier1Supplies, Washington, Iowa) was used in attempts to exclude coyotes from some release sites during some years. ElectroNet is 107 cm in height, powered by 12-V deep cycle batteries, and constructed with 10 alternately charged conductors supported with vertical plastic stays every 30 cm. ElectroNet is designed to exclude mammalian species the size of coyotes and badgers while allowing ferrets and other smaller mammals to move through the fence. Experimental trials of ElectroNet excluded coyotes from bait stations for up to 2 weeks (Matchett, 1995), and telemetry data from ferret reintroduction sites indicated that ElectroNet may have enhanced short-term survival of ferrets within fenced enclosures (Matchett, 1999). We tried to extend knowledge of the utility of ElectroNet by testing for differences in both short- and long-term minimum survival between those reintroduction sites that used ElectroNet and those that did not (table 1). The perimeter of fencing used at reintroduction sites varied from 3.5 km to 13 km and was maintained for a minimum of 30 days postrelease.

We hypothesized that ferrets in areas with higher densities of prairie dogs (i.e., South Dakota), higher levels of coyote control, and electric fencing would have higher estimates of both short- and long-term survival. We generated linear models to evaluate this prediction; competing models included interaction terms and combinations of four explanatory variables (see tables 2 and 3 for a complete list of models). We used likelihood-based methods (Buckland and others, 1997; Burnham and Anderson, 1998) to quantify strength of evidence for alternative models explaining patterns of ferret survival. Estimating the "weight," or probability that a given model is the best approximation to truth among the models considered, is a means for reporting the relative support for alternative models where the weights from the candidate list of models sum to 1. Thus a model with a weight of 1 has complete support and a model with a weight of 0 has no support (Burnham and Anderson, 1998).

We used Proc GENMOD with the logit link option, which assumes a binomial distribution (SAS Institute Inc., 1999) to analyze each model and create output required to

Table 1. Descriptive data on black-footed ferret (*Mustela nigripes*) survival (short-term = 30 days, long-term = 6–8 months) and predator control efforts (high, medium, or low) from 20 release sites in Montana and South Dakota.

Release area and year	Number of ferrets released	Short-term survival	Long-term survival	Number of coyotes removed	Electric fence used?
MT 94	17	0.47	0.41	Medium	No
MT 95	33	0.61	0.33	High	Yes
MT 96	39	0.56	0.15	High	Yes
MT 97	20	0.55	0.20	Medium	Yes
MT 98	21	0.43	0.14	Medium	Yes
MT 99	23	0.35	0.04	Medium	Yes
MT 01 (BLM 40)	20	0.40	0.15	Low	Yes
MT 02 (BLM 40)	25	0.32	0.16	Low	No
MT 03	37	0.76	0.38	Low	No
MT 03 (BLM 40)	20	0.20	missing	Low	No
SD 94	13	0.38	0.23	Medium	No
SD 95	37	0.30	0.08	Medium	No
SD 96 (Agate)	15	0.53	0.07	High	Yes
SD 96 (Burns)	24	0.29	0.13	High	Yes
SD 97 (Kosher)	21	0.76	0.24	Medium	Yes
SD 97 (Sage)	36	0.86	0.69	Medium	Yes
SD 98 (Agate)	25	0.88	0.28	Low	No
SD 98 (Sage)	15	0.73	0.33	Low	No
SD 99 (Hecktable)	36	0.86	0.44	Low	No
SD 99 (Sage)	12	0.75	0.50	Medium	No

calculate Akaike's Information Criterion (AIC) values. We used ferrets as replicates (n=489) and performed a separate analysis for short- and long-term survival data. For each analysis we assessed the goodness-of-fit by calculating the deviance on the global (fully parameterized) model. We used \hat{c} (deviance/df) to adjust for overdispersion (i.e., lack of fit) and used the small-sample correction of AIC (QAIC_c; Lebreton and others, 1992; Burnham and Anderson, 1998) to rank the models and generate an estimate of the weight. We based inferences of survival on the top model.

Results

General patterns in the data show that: (1) both shortand long-term minimum survival estimates have increased in latter years of reintroduction efforts (this was especially true in South Dakota; see table 1); and (2) there was a great deal of variation in estimates of survival across sites and years (short-term low = 20 percent, short-term high = 88 percent; long-term low = 4 percent, long-term high = 69 percent).

Deviance for both global models (short- and long-term analyses) was large (35.5 and 32.7, respectively; P < 0.001) indicating that overdispersion was problematic (i.e., fit of model was not good). Based on QAIC, weights (tables 2 and 3), both short- and long-term minimum survival of reintroduced ferrets were supported by models showing a difference primarily between levels of coyote control and fencing. Ferret survival was inversely related to coyote control with releases that had the highest levels of control showing approximately 12 percent lower minimum survival compared to the lowest levels of control for both short- and long-term analyses (figs. 1 and 2). Evidence of the effectiveness of electric fencing was opposite of what we predicted; ferrets released in areas with fencing showed lower short- and long-term minimum survival than ferrets released in areas without fencing, 3 percent and 5 percent, respectively (figs. 1 and 2). The variable site was not a factor in either analysis, indicating no detectable differences in minimum survival between release sites. There was only weak evidence that survival of ferrets differed between States (i.e., the variable State was part of the 2nd ranked model in the long-term analysis; table 3), indicating differences in prairie dog density between States did not appear to influence survival.

206 Recovery of the Black-footed Ferret

Table 2. Results of the Akaike's Information Criterion (AIC) model selection procedure to determine the model that best explains 1-month survival patterns of reintroduced black-footed ferrets (*Mustela nigripes*), 1994–2003. NPAR is the number of parameters, QAIC_c is a version of AIC adjusted for overdispersion, DELQAIC_c is the difference in QAIC relative to the smallest value in the set, and Weight is an estimate of the likelihood of each model (Burnham and Anderson, 1998). Variables in the models are: fence (present or not), coyote (level of lethal coyote control: low, medium, high), State (Montana or South Dakota), and site (eight different release sites). Dot indicates a model that only includes an intercept (i.e., no explanatory variables). The symbol * indicates an interaction between two variables, and | indicates all possible combinations of the variables.

Model	NPAR	OAIC _c	DELQAIC _c	Weight
Fence coyote	4	123.41	0.00	0.51
Fence	2	124.93	1.52	0.24
Coyote	3	125.55	2.14	0.18
Dot	1	128.85	5.44	0.03
State fence State*fence	4	129.00	5.59	0.03
Fence coyote fence*coyote	5	132.18	8.77	0.01
State fence	3	133.20	9.79	0.00
State coyote	4	136.25	12.84	0.00
State	2	137.76	14.34	0.00
State fence coyote	5	139.17	15.76	0.00
State coyote State*coyote	6	166.83	43.42	0.00
State fence State coyote fence coyote	9	222.85	99.44	0.00
Site	8	346.79	223.38	0.00

Table 3. Results of the Akaike's Information Criterion (AIC) model selection procedure to determine the model that best explains long-term (6–8 months) survival patterns of reintroduced black-footed ferrets (*Mustela nigripes*), 1994–2003. NPAR is the number of parameters, QAIC, is a version of AIC adjusted for overdispersion, DELQAIC, is the difference in QAIC relative to the smallest value in the set, and Weight is an estimate of the likelihood of each model (Burnham and Anderson, 1998). Variables in the models are: fence (present or not), coyote (level of lethal coyote control: low, medium, high), State (Montana or South Dakota), and site (eight different release sites). Dot indicates a model with only an intercept (i.e., no explanatory variables). The symbol * indicates an interaction between two variables, and | indicates all possible combinations of the variables.

Model	NPAR	OAIC _c	DELQAIC _c	Weight
Fence coyote	4	130.67	0.00	0.484
State fence coyote	5	132.98	2.30	0.153
Fence coyote fence*coyote	5	133.16	2.48	0.140
Fence	2	134.31	3.64	0.078
Coyote	3	135.39	4.72	0.046
State fence	3	135.47	4.80	0.044
Dot	1	136.68	6.00	0.024
State coyote	4	138.84	6.17	0.022
State	2	139.60	8.93	0.006
State fence State*fence	4	140.79	10.12	0.003
State coyote State*coyote	6	143.15	12.47	0.001
State fence State coyote fence coyote	9	193.08	62.41	0.000
Site	8	227.04	96.37	0.000

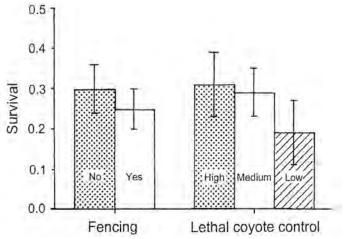


Figure 1. Estimates of short-term (1 month) minimum survival of reintroduced black-footed ferrets (*Mustela nigripes*) for two explanatory variables: fencing (present or not) and lethal coyote control (low, medium, and high). In total, 489 ferrets were released from different sites in Montana and South Dakota from 1994 to 2003. Error bars represent 95% confidence intervals.

Discussion

A general pattern that emerged from the data was that estimates of both short- and long-term survival were highly variable even in later years of releases. Variation in survival could be due to a number of factors, including differences in habitat quality, random variation, measurement error, and differences in predation pressure. One factor relating to predators that may have contributed to variation in survival estimates is the role of one or a few problem individuals. Here we define problem individuals as predators that seem to develop a search image for ferrets, consequently becoming disproportionately more successful than other predators at finding and killing ferrets. Critical to the discussion of problem individuals is the realization that mortality of single animals has a larger effect in small populations than in larger populations (Krebs and others, 1995; Krebs, 1996). Thus, it is possible for one or a few individual predators to have a large overall effect on a small population of reintroduced ferrets. A likely example of problem individuals was seen in South Dakota during the 1996 releases (table 1). Nearly half (11 of 24) of the known mortalities that occurred during that release season were caused by one to three great horned owls. In response to the identified problem, three great horned owls were killed on and around the release site, and no further known mortalities were caused by owls. Problem individuals could explain the pattern observed in Montana in 2003 where one release site had a high short-term survival rate of 76 percent while the other had short-term survival of 20 percent, even though no predation by owls was observed.

Our analyses indicated that the relationship between the level of lethal coyote control and ferret survival was opposite of what we hypothesized; that is, more intensive efforts to remove coyotes related to poorer survival for ferrets. This

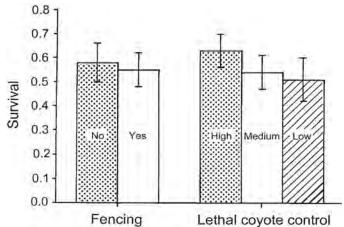


Figure 2. Estimates of long-term (6–8 months) minimum survival of reintroduced black-footed ferrets (*Mustela nigripes*) for two explanatory variables: fencing (present or not) and lethal coyote control (low, medium, and high). In total, 489 ferrets were released from different sites in Montana and South Dakota from 1994 to 2003. Error bars represent 95% confidence intervals.

relationship was apparent for both short- and long-term data (figs. 1 and 2). However, several factors are important to consider before drawing any conclusions regarding these patterns. First, most of the high-level efforts for controlling coyotes occurred in earlier years of releases. Thus, the general increase in estimates of survival over time could reflect improvements in preconditioning of ferrets rather than changes in coyote control. Although no data exist to quantify the "quality" of ferrets released over time, it seems possible that preconditioning programs could have improved as the programs were optimized. Second, our method for categorizing levels of coyote control was not ideal. If future research addresses this question, then quantifying density of coyotes pre- and postremoval would be paramount for relating coyote control to ferret survival. Third, increasing survival over successive years may be an artifact of increasing observer efficiency at detecting ferrets or other factors related to estimating survival. The fundamental problem that gives rise to interpretative difficulties mentioned in factors 1-3 previously (and others) is the unbalanced design. All treatments were not replicated at all sites and certainly not in all years at all sites. For example, the BLM 40 complex had only "low" predator control for all 3 years that ferrets were released. Site-specific impacts of unmeasured factors (e.g., disease) may be misinterpreted as treatment effects. Finally, some of the confusion regarding the effectiveness of predator management stems from poor understanding of coyote ecology and behavior in and around release sites. Almost no reliable information exists on activity patterns, use of prairie dog habitat by coyotes, and response of coyotes to control efforts as it relates to blackfooted ferrets.

Nevertheless, it is interesting to speculate on how higher levels of coyote control could cause a decrease in ferret survival. Assuming that killing coyotes creates voids filled by coyotes from surrounding territories, one possibility is that as new individuals begin to establish territories, their movements and behavior enhance the probability of encountering ferrets. Many of the ferrets that have been found killed by coyotes were not eaten, indicating that the interaction between coyotes and ferrets may more accurately be described as a form of competition (i.e., intraguild predation; Holt and Polis, 1997; Palomares and Caro, 1999). In competitive interactions, individual animals may not develop specific search images for competitors but rather respond to competitors in an opportunistic fashion. Creating situations in which coyotes are more active (i.e., filling voids) may enhance encounter rates and create greater threat for ferrets.

Of the tools used to control coyote predation, electric fencing offered the most potential to completely eliminate coyote predation on ferrets. The general impression from biologists working at release sites was that fencing did exclude coyotes. At minimum we expected to see higher short-term survival rates for ferrets at sites that used fencing. We found no evidence, however, that fencing enhanced ferret survival for the short- or long-term; in fact, we detected slightly lower survival rates (figs. 1 and 2) at sites that used fencing. Again we caution against strong interpretation of these data for reasons already mentioned, but a couple of factors may explain this pattern.

First, fencing was only used during earlier years of reintroductions (table 1). Though we tried to control for preconditioning in this analysis, it is possible that ferrets released in later years had better preconditioning that enhanced their survival. Second, we know great horned owl predation had a large effect on survival of ferrets at two sites (Agate and Burns) in South Dakota in 1996, both sites that used fencing. Fencing does not deter avian predation, and in this analysis we were unable to control for owl or other avian predation. If we could have controlled for avian predation, it is possible that we would have detected higher survival of ferrets released in areas with fencing, at least for the short-term. Finally, in years when fencing was used, anecdotal observations indicate that many of the ferrets killed by coyotes occurred when ferrets moved outside the fence boundary. Again we were unable to control for this confounding factor in this analysis.

Our results highlight the need to perform well designed experiments to better elucidate the possible benefit of predator management to enhance black-footed ferret survival at reintroduction sites. The fact that survival of reintroduced ferrets remains highly variable indicates that factors other than preconditioning are important. Based on our understanding of ferret ecology, it is likely that predation is responsible for most of the mortality. Understanding whether or not we can manage this predation pressure remains an important goal for ferret recovery. Equally important to recovery efforts is the need to understand the role that predation plays in established populations of black-footed ferrets. Such data would not only provide direct benefits to ferret conservation by potentially increasing the number of ferrets that could be translocated but would also provide better parameter estimates for modeling exercises that depend upon understanding the role of important ecological forces. The most effective means for determining the role of predation in ferret demography and ecology would be to manipulate predator populations and compare responses to unmanipulated populations. Because coyotes are the most important predator of ferrets, we suggest using electric fencing to exclude coyotes as it offers the most potential to control coyote predation.

For the manager who must decide whether or not to manage predators in and around reintroduction sites, we offer the following recommendations. First, great horned owls view ferrets as prey and probably can develop a search image for ferrets. Problem individuals may have large impacts on a population of reintroduced ferrets. If great horned owls are present in the immediate vicinity of a release area, it may be wise to remove individual owls, and, if possible, remove perch sites as well. Second, there is no evidence that lethal removal of coyotes at the levels of control implemented in previous releases enhances short- or long-term survival of ferrets. Extensive control efforts may eliminate coyotes from release sites, temporarily reducing predation pressure on ferrets. However, rates of recolonization by coyotes after such removal are poorly understood and may have important implications for ferrets. Lethal removal of a few individual coyotes probably will not enhance ferret survival because coyotes are often abundant and possibly because of the way coyotes and ferrets interact. Last, electric fencing appears to be an effective method for excluding coyotes and may offer benefits for reintroduced ferrets as long as the fencing is up and functioning. However, maintaining fencing over the long-term is difficult and expensive; thus, fencing is generally only used for short periods (1–2 months). Once fencing is removed, there is no evidence to suggest that the short-term benefits translate into enhanced long-term survival. Thus, for future reintroductions we do not recommend fencing unless the manager can maintain it for long periods or identify how short-term protection may aid long-term survival of ferrets.

References Cited

Biggins, D.E., 2000, Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmannii*)—conservation and evolutionary implications: Fort Collins, Colorado State University, Ph.D. dissertation, 184 p.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., and Vargas, A., 1998, The effect of rearing methods on survival of reintroduced black-footed ferrets: Journal of Wildlife Management, v. 62, p. 643–653.

Biggins, D.E., Hanebury, L.R., and Miller, B.J., 1991, Trial release of Siberian polecats (*Mustela eversmanni*): Fort Collins, Colo., U.S. Fish and Wildlife Service, National Ecology Research Center, 25 p.

- Biggins, D.E., Vargas, A., Godbey, J.L., and Anderson, S.H., 1999, Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*): Biological Conservation, v. 89, p. 121–129.
- Buckland, S.T., Burnham, K.P., and Augustin, N.H., 1997, Model selection—an integral part of inference: Biometrics, v. 53, p. 603–618.
- Burnham, K.P., and Anderson, D.R., 1998, Model selection and inference—a practical information-theoretic approach: New York, Springer-Verlag, 353 p.
- Campbell, T.M., III, Biggins, D., Forrest, S., and Clark, T.W., 1985, Spotlighting as a method to locate and study blackfooted ferrets, *in* Anderson, S.H., and Inkley, D.B., eds., Black-footed ferret workshop proceedings: Cheyenne, Wyoming Game and Fish Department, p. 24.1–24.7.
- Estes, J., Crooks, K., and Holt, R., 2001, Ecological role of predators, *in* Levin, S.A., ed., Encyclopedia of biodiversity: San Diego, Calif., Academic Press, p. 857–878.
- Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., III, Fagerstone, K.A., and Thorne, E.T., 1988, Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985: Journal of Mammalogy, v. 69, p. 261–273.
- Holt, R.D., and Polis, G.A., 1997, A theoretical framework for intraguild predation: American Naturalist, v. 149, p. 745–764.
- Krebs, C.J., Boonstra, R., and Kenney, A.J., 1995, Population dynamics of the collared lemming and the tundra vole

- at Pearce Point, Northwest Territories, Canada: Oecologia, v. 103, p. 481–489.
- Krebs, C.J., 1996, Population cycles revisited: Journal of Mammalogy, v. 77, p. 8–24.
- Lebreton, J.D., Burnham, K.P., Colbert, J., and Anderson, D.R., 1992, Modeling survival and testing biological hypotheses using marked animals—a unified approach with case studies: Ecological Monographs, v. 62, p. 67–118.
- Matchett, M.R., 1995, Trials of electronet fencing to exclude coyotes: Lewistown, Mont., U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, 7 p.
- Matchett, M.R., 1999, Black-footed ferret recovery activities on the UL Bend and Charles M. Russell National Wildlife Refuges, Phillips County, Montana—1998 annual report and 5-year summary: Lewistown, Mont., U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, 22 p.
- Palomares, F., and Caro, T.M., 1999, Interspecific killing among mammalian carnivores: American Naturalist, v. 153, p. 492–508.
- SAS Institute Inc., 1999, SAS OnlineDoc[®], Version 8: Cary, N.C., SAS Institute Inc.
- Terborgh, J.J., Estes, J.A., Paquet, P.C., Ralls, K., Boyd-Heger, D., Miller, D., and Noss, R., 1999, The role of top carnivores in regulating terrestrial ecosystems, *in* Soulé, M.E., and Terborgh, J., eds., Continental conservation—scientific foundations of regional reserve networks: Washington, D.C., Island Press, p. 39–64.

