Journal of Mammalogy, 92(4):732–741, 2011

Landscape features influence postrelease predation on endangered black-footed ferrets

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Predation can be a critical factor influencing recovery of endangered species. In most recovery efforts lethal and nonlethal influences of predators are not sufficiently understood to allow prediction of predation risk, despite its importance. We investigated whether landscape features could be used to model predation risk from coyotes (*Canis latrans*) and great horned owls (*Bubo virginianus*) on the endangered black-footed ferret (*Mustela nigripes*). We used location data of reintroduced ferrets from 3 sites in South Dakota to determine whether exposure to landscape features typically associated with predators affected survival of ferrets, and whether ferrets considered predation risk when choosing habitat near perches potentially used by owls or near linear features predicted to be used by coyotes. Exposure to areas near likely owl perches reduced ferret survival, but landscape features potentially associated with coyote movements had no appreciable effect on survival. Ferrets were located within 90 m of perches more than expected in 2 study sites that also had higher ferret mortality due to owl predation. Densities of potential coyote travel routes near ferret locations were no different than expected in all 3 sites. Repatriated ferrets might have selected resources based on factors other than predator avoidance. Considering an easily quantified landscape feature (i.e., owl perches) can enhance success of reintroduction efforts for ferrets. Nonetheless, development of predictive models of predation risk and management strategies to mitigate that risk is not necessarily straightforward for more generalist predators such as coyotes.

Key words: *Bubo virginianus*, *Canis latrans*, coyote, great horned owl, habitat selection, *Mustela nigripes*, predation risk

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DOI: 10.1644/10-MAMM-S-061.1

Predation can have both lethal effects and nonlethal behavioral influences that affect prey populations, community dynamics, and functioning of entire ecosystems (Estes et al. 2001; Lima 1998; Lima and Dill 1990). Lethal effects of predation reduce survival and can restrict distribution or reduce abundance of prey (Krebs 2001). Nonlethal influences of predation primarily include behavioral changes of prey in response to predation risk; animals might be able to assess their predation risk, integrate this information into their decision-making processes, and alter their behavior so they become more difficult for predators to capture or detect (Lima 1998; Lima and Dill 1990). Such decision-making reflects trade-offs between the benefits of engaging in an activity (e.g., energy intake from foraging) and the costs of that activity (e.g., an early death from predation), potentially leading animals to choose habitat that is safer from predators but less

energetically profitable (Lima 1998; Lima and Dill 1990). These behavioral changes are the basis for the ''ecology of fear concept'' (Brown et al. 1999; Ripple and Beschta 2004). Animals can respond to predation risk by avoiding predators, avoiding specific habitats likely used by predators, or accepting predation risk in the pursuit of resources. These behaviorally mediated, nonlethal interactions between predators and prey can play an important role in the structure of ecological systems (Lima 1998; Ripple and Beschta 2004).

Despite considerable knowledge of predators and their prey, biologists generally lack the ability to predict predation risk. Greater predictive power can be gained from considering landscape features associated with predators. For example, Thompson and Gese (2007) observed behavioral avoidance in swift foxes of landscape features that increased predation risk from coyotes, suggesting that landscape structure can play a critical role in moderating predation. Kauffman et al. (2007) demonstrated that, in some cases, predation can be influenced more strongly by landscape features than by distribution of predators. Hence, understanding how spatial variation in landscape structure influences predation patterns likely can offer opportunities for predicting predation risk.

Predation can be a critically important factor to consider for recovery of endangered species (Carpenter and Mueller 2008; Jenny et al. 2004). Predation plays an important role in the survival of both wild-born and reintroduced black-footed ferrets (hereafter, ferrets; *Mustela nigripes*). These highly endangered mustelids, nocturnal habitat specialists that rely on prairie dogs (*Cynomys* spp.) for food and their burrows for shelter (Biggins et al. 1998), currently are being recovered through an intensive captive-breeding and reintroduction program. Predation was the primary cause of ferret mortality in a wild-born population (Forrest et al. 1988) and caused up to 95% of the mortality of reintroduced ferrets (Biggins et al. 2006b; Breck et al. 2006). Coyotes (*Canis latrans*) and great horned owls (*Bubo virginianus*) have been primary predators of ferrets (Henderson et al. 1974); coyotes caused the largest number of ferret deaths at reintroduction sites, with significant predation by great horned owls as well (Breck et al. 2006). Mortality of ferrets from these predators might be linked to various landscape variables, such as perching structures and predator travel routes. Because of the immense threat posed by predators, ferrets provide an excellent study species for better understanding if and how landscape features can be used to predict the impacts of predators.

Our 1st objective was to determine whether landscape features typically associated with the perching behavior of great horned owls (i.e., trees, mounds, and fence posts) and coyote movement (i.e., roads, fence lines, and drainages) affected survival of reintroduced ferrets. As a corollary to this objective, we took advantage of efforts to mitigate coyote predation and tested whether electric fences designed to exclude coyotes influenced ferret survival. Our 2nd objective was to determine whether habitat selection by newly released ferrets was influenced by predation risk. Although ferrets restrict their space use to prairie dog colonies, they might exhibit important trade-offs between maximizing prey resources and minimizing predation risk within these colonies. We hypothesized that exposure to landscape features predicted to be favored by predators would affect the survival of ferrets and that ferrets would select habitat less exposed to these features than would be expected at random.

Materials and Methods

Study area.—We conducted this study in the Conata Basin/Badlands area, located in southern South Dakota on public lands, administered by the United States Forest Service (Buffalo Gap National Grassland) and the National Park Service (Badlands National Park), and on adjoining private lands. The study focused on 3 sites (Fig. 1): Sage Creek, located in the western portion of Conata Basin on the Buffalo Gap National Grassland (43°45′N, 102°18′W); Agate, located in the eastern portion of Conata Basin (43°46′N, 102°9′W); and Burns Basin, located in Badlands National Park (43°47′N, 102°7′W). This area is a mixed-grass prairie ecosystem dominated by western wheatgrass (*Pascopyrum smithii*), buffalograss (*Bouteloua dactyloides*), and blue grama (*Bouteloua gracilis*—Severson and Plumb 1998). Colonies of black-tailed prairie dogs are dispersed throughout the area. Topography is mostly level but dissected by drainages that generally run north to south and contain cottonwoods (*Populus deltoides*). Roads and fences are present throughout the area, and several badlands formations (mounds or buttes) are scattered on the sites.

Data collection.—Captive ferrets born in 1996 and 1997 were raised at the National Black-footed Ferret Conservation Center in Sybille, Wyoming, at the Louisville Zoological Gardens in Louisville, Kentucky, and at the Phoenix Zoo in Phoenix, Arizona. We collared ferrets with radiotransmitters attached to wool collars sewn with cotton thread (Biggins et al. 2006a), then released them into each of the 3 sites in Conata Basin/Badlands. We collected radiotelemetry data on 79 ferrets via triangulation (Biggins et al. 2006a, 2006d), monitoring ferrets in Agate from 25 September to 9 October 1996, in Burns Basin from 16 October to 29 October 1996, and in Sage Creek from 3 October to 5 November 1997. The Sage Creek ferrets were released in 2 different cohorts, the 1st on 3 October 1997 and the 2nd on 22 October 1997. Telemetric monitoring of ferrets usually is conducted for short time periods because of costs and potential risks of transmitter collars to the animals (Biggins et al. 2006a, 2006c), and because the first 2 weeks postrelease are critical regarding movements and mortality (Biggins 2000). Monitoring of ferrets occurred nightly, and each animal was tracked every 5–30 min. On average, each ferret was located above ground 68% (± 3% *SE*) of the nights monitored. To determine the status of ferrets we relied on radiosignal fluctuations or lack thereof, and we investigated any ferrets that remained in 1 location for an extended period of time (>2 h). We categorized mortalities of individuals as killed by coyotes, raptors, badgers (*Taxidea taxus*), unknown predators, starva-

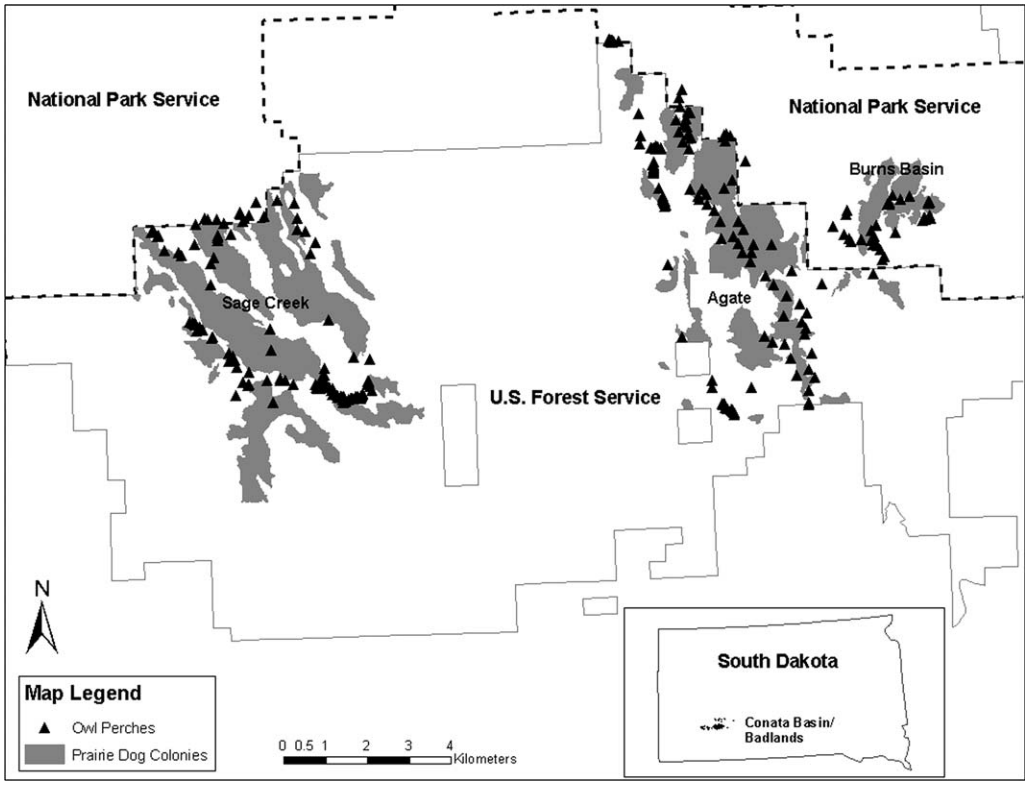

Fig. 1.—Map of prairie dog colonies, including potential great horned owl (*Bubo virginianus*) perches, in Conata Basin/Badlands, South Dakota, 1996 (Sage Creek and Agate) and 1993 (Burns Basin). Only those colonies that were surveyed for owl perches are shown.

tion, or disease. Predation by great horned owls was differentiated from that by diurnal raptors by estimating the time of death from the radiotelemetry data. Collars wore rapidly and either fell off or were removed at the end of the study. We included data for 25 ferrets in Agate (15 males and 10 females), 18 ferrets in Burns Basin (10 males and 8 females), and 36 ferrets in Sage Creek (20 males and 16 females). Our total sample size of 79 ferrets was substantial considering that ferrets were exceedingly rare in both captivity and the wild at that time. Our procedures conformed to guidelines for animal care and use approved by the American Society of Mammalogists that were published later (Gannon et al. 2007), were approved by the Animal Care and Use Committee at the United States Geological Survey, and were carried out under endangered species permit PRT-704930 issued by Region 6 of the United States Fish and Wildlife Service.

In July 2007 and June 2008 we collected global positioning system data on the locations of potential great horned owl perches in Agate, Burns Basin, and Sage Creek. Great horned owls are primarily nocturnal perch hunters (Houston et al. 1998); hence, we defined likely owl perches (hereafter, perches) in Conata Basin/Badlands as any elevated structure on the landscape, which included trees, mounds, buttes, and prominent fence posts. Trees located within an eroded drainage were not included if the tops of such trees were below the edge of the drainage; all trees located outside of a drainage were included in the data collection. All mounds $\geq$ 2 m in height located on each site were included. Only elevated fence posts with a height $\geq$ 3 m were included, assuming these would be preferred by owls; these posts occurred sporadically throughout the fence lines and were taller than the numerous standard posts along the fences, which were approximately 1 m high. Anecdotal evidence of owl use of perches included owl sightings and pellets found beneath certain trees.

Coyotes readily use landscape features such as roads, fences, rivers, and drainage ditches as travel corridors, protective cover, and areas for hunting (Atwood 2006; Atwood et al. 2004; Linhart and Knowlton 1975; Young et al. 2006). Coyotes kill ferrets opportunistically when traveling along these linear features, rather than actively hunt them, an idea supported by the observation that ferrets usually are not eaten by coyotes that kill them (Breck et al. 2006). We therefore hypothesized that roads, fence lines, and drainages (hereafter, linear features) in Conata Basin/Badlands might be potential travel routes for coyotes and, therefore, might predict ferret predation risk and habitat selection. Anecdotal evidence of coyote use of linear features included coyote sightings, tracks, and scat along roads, fence lines, and drainages. We obtained geographic information system data on the locations of linear features from the United States Forest Service. Even though we collected landscape data for both owls and coyotes approximately 10 years after the ferret radiotelemetry data, we have conducted research continuously on the study area since ferret release and know that most landscape structures, including roads and fences, have not changed substantially during this time. Further, management of these areas has

remained constant, and no significant land changes (e.g., timber harvest or removal, plowing, or development) have occurred.

A low-to-moderate intensity of lethal coyote control occurred in and around the study area approximately 2–3 weeks before ferrets were released each year, with a higher level of control in Agate and Burns Basin than in Sage Creek. We are uncertain how these removal efforts affected the coyote population, although anecdotal evidence suggested that effectiveness was limited (Breck et al. 2006). Additionally, electric fences (ElectroNet, Premier1Supplies, Washington, Iowa) of 107 cm in height were installed in conjunction with another project (Breck et al. 2006) in parts of the study area to exclude coyotes from ferret release sites but allow passage of ferrets. One fence was placed in Agate, 1 fence in Burns Basin, and 2 fences in Sage Creek. The total area inside the 4 fences was 7.9 km^2 (2.0 km^2 per fence $\pm$ 0.5 *SE*). Fencing was installed and activated 1–2 weeks prior to the release of ferrets, and we attempted to remove terrestrial predators left within the enclosures. The fences were supported by vertical plastic stays every 30 cm, which were too small and flexible to function as perches for great horned owls. Global positioning system data defined the perimeters of electric fences, which we used to analyze separately the effect of these fences on ferret survival.

Survival analyses.—We characterized exposure to perches and linear features using nearest-neighbor and buffer analyses (ArcMap version 9.2; ESRI, Redlands, California). The nearest-neighbor analysis involved calculating the distance from each ferret location to the nearest perch and linear feature, followed by computing a ferret-specific average for each feature. We then analyzed the relationship between probability of survival of ferrets and the average distance of ferret locations from these features.

The buffer analysis was conducted for perches by calculating buffers of 90 m, the reported effective hunting distance of a great horned owl from an elevated perch (Houston et al. 1998; Petersen 1979), around each perch. We then calculated the percentage of all telemetry locations for each ferret within these buffers. For the linear features we computed 100-m buffers around each ferret location. Lingle and Wilson (2001) demonstrated that coyotes approached deer at distances $<$ 200 m during the day, but our study focused on coyote predation on smaller prey and at night, when coyote visual acuity is lower (Kavanau and Ramos 1975), suggesting a smaller buffer. For each ferret we calculated the density of linear features within the 100-m buffers by dividing the length of the features by the area of the buffer, and then we computed a ferret-specific average density. We followed Baschieri (2007) and Johnson and Collinge (2004) for calculation of road densities. To test our choice of buffer radius we also calculated densities within buffers of 50 m and 200 m and obtained similar results, so only the results for the 100-m buffers are reported here. Thus, the buffer analyses modeled probability of survival of ferrets as a continuous function of the proportion of ferret locations inside buffers around perches (for the owl analyses) and as a continuous function of linear features inside buffers around ferret locations (for the coyote analyses). In addition, we estimated potential predation risk from coyotes by calculating, for each ferret, the percentage of all telemetry locations outside the electric fences (where ferrets were expected to be more exposed to coyote predation).

We conducted survival analyses in program MARK with the KNOWN FATES option (White and Burnham 1999), using the first 13 days of radiotracking for each ferret. For each ferret-day we classified the ferret as either alive or dead, or censored if the radiosignal was not detected during that day. Because ferret mortalities occurred due to several causes, and our analyses focused only on great horned owl and coyote predation, we divided the analyses into 2 data sets: ferrets killed by owls were considered dead on the day they were killed, but ferrets killed by other predators were censored on the day they were killed and all successive days (owl data set); and ferrets killed by coyotes were considered dead on the day they were killed, but ferrets killed by other predators were censored on the day they were killed and all successive days (coyote data set).

In the survival analyses we included sex as an attribute group for both the owl and coyote data sets. For the owl data set we included distances to perches and percentages of ferret locations within buffers of perches as covariates. For the coyote data set we included distances to linear features, densities of linear features within buffers of ferret locations, and percentages of ferret locations outside the electric fences as covariates. These 5 landscape measures varied considerably among the 3 sites; other characteristics, such as topography and habitat, generally were similar and were not analyzed. For each data set we 1st tested for any differences in survival due to sex (Table 1; owl data set models 3 and 4; coyote data set models 5 and 8) by choosing the most parsimonious model based on the Akaike's information criterion value corrected for low sample size (AIC_c—Akaike 1973; Burnham and Anderson 2002). Using the most parsimonious model (Table 1, models 3 and 5; see ''Results''), we then added each of the 2 covariates separately for the owl data set to generate 2 additional models (Table 1, models 1 and 2) and each of the 3 covariates separately for the coyote data set to generate 3 additional models (Table 1, models 6, 7, and 9). Because the 2 perch covariates were correlated with each other (Pearson $r = -0.62$, $n = 79$, $P < 0.001$), and the 2 linear-feature covariates also were correlated with each other (Pearson $r = -0.35$, $n = 79$, $P = 0.001$), we did not run combined models including both covariates for the respective owl and coyote data sets. The electric-fence covariate was not correlated with either linear-feature covariate (distance covariate: Pearson $r = 0.15$, $n = 79$, $P = 0.184$; buffer covariate: Pearson $r = -0.15$, $n = 79$, $P = 0.183$); thus, we ran 2 additional models for the coyote data set, 1 model including the distance and electric-fence covariates (Table 1, model 11) and 1 model including the buffer and electric-fence covariates (Table 1, model 10). We then selected the model in each data set with the smallest AIC_c value as the best model for predicting ferret survival

Table 1.—Alternate models and model selection statistics considered for estimating survival rates of reintroduced black-footed ferrets (*Mustela nigripes*) radiocollared in Conata Basin/Badlands, South Dakota, 1996 and 1997, that were killed by great horned owls (*Bubo virginianus*) and coyotes (*Canis latrans*). Sex classes were male (M) and female (F). (MvF) models estimated survival separately for each sex; (M=F) models estimated survival conjointly for both sexes. Covariates included percentages of ferret locations within 90-m buffers of potential great horned owl perches (OwlBuff), distances from ferret locations to the nearest perches (OwlDist), densities of linear features predicted to be used by coyotes within 100-m buffers of ferret locations (CoyoteBuff), distances from ferret locations to the nearest linear features (CoyoteDist), and percentages of ferret locations outside electric fences (ElecFences).

Model	Model structure	AIC_c	ΔAIC_c	w_i	k[a]
Survival of black-footed ferrets killed by great horned owls					
1	S(M=F, OwlBuff)	73.9	0.0	0.758	2
2	S(M=F, OwlDist)	76.2	2.3	0.238	2
3	S(M=F)	85.5	11.6	0.002	1
4	S(MvF)	86.5	12.6	0.001	2
Survival of black-footed ferrets killed by coyotes					
5	S(M=F)	101.8	0.0	0.354	1
6	S(M=F, CoyoteBuff)	103.6	1.8	0.146	2
7	S(M=F, CoyoteDist)	103.7	1.9	0.137	2
8	S(MvF)	103.8	2.0	0.130	2
9	S(M=F, ElecFences)	103.8	2.0	0.130	2
10	S(M=F, CoyoteBuff, ElecFences)	105.6	3.8	0.053	3
11	S(M=F, CoyoteDist, ElecFences)	105.7	3.9	0.050	3

[a] k = the number of parameters estimated by each model.

(Burnham and Anderson 2002). As additional evidence for the best model, we examined the effect size of the covariate (if the best model included a covariate) by determining whether the 90% confidence interval (90% *CI*) of the covariate coefficient included 0 (program MARK version 5.1—White and Burnham 1999). We considered models with $\Delta AIC_c < 2$ to have substantial empirical support, ΔAIC_c of 4–7 to have considerably less support, and $\Delta AIC_c > 10$ to have essentially no support (Burnham and Anderson 2002).

Habitat-selection analyses.—We analyzed habitat selection by ferrets with use-availability data within activity areas of ferrets (areas of use by individual ferrets; 3rd-order selection—Johnson 1980) and selection of activity areas within the study area (2nd-order selection—Johnson 1980). Within each scale we conducted analyses using the individual ferret as the sampling unit (Biggins et al. 2006d), rendering autocorrelation of repeated locations irrelevant, assuming that locations for a given individual represent its movements throughout the habitat during the study period (Otis and White 1999). We conducted the habitat-selection analyses based on ferret exposure to perches and linear features analyzed independently. We focused the habitat-selection analysis involving perches on the percentage of ferret locations found within the 90-m buffers of perches because the best model for predicting ferret survival in the owl data set included the buffer covariate (see ''Results''). We focused the habitat-selection analysis involving linear features on the average feature density found within the 100-m buffers of ferret locations because the best model in the coyote data set that included a covariate incorporated the buffer covariate (see ''Results''). For these analyses we combined the Agate and Burns Basin sites into 1 study area, because several ferrets had locations overlapping both sites.

For the analyses at the activity-area scale, and for each of the 2 study sites (Agate/Burns Basin and Sage Creek), we calculated minimum convex polygons for each ferret and selected random points within each minimum convex polygon, using the same number as each individual ferret's locations (Agate/Burns Basin: n = 2,656 total locations, range 4–203 locations, 62 locations per individual ± 8.9 *SE*; Sage Creek: n = 1,428 total locations, range 4–117 locations, 40 ± 4.4 locations per individual). For the perch analysis we calculated for each individual the percentage of actual and random locations within the 90-m buffers, comparing them with a paired *t*-test for each study site. For the linear-feature analysis we calculated for each individual the average feature density found within 100-m buffers of ferret and random locations, comparing them with a paired *t*-test for each study site.

For the analyses at the study-area scale only those ferret locations occurring on prairie dog colonies were included; off-colony locations do not imply that ferrets actually reside in these areas because ferrets will make exploratory moves to assess prairie dog distribution and also occasionally will travel between colonies (Biggins et al. 2006d). For each site we 1st determined which colonies each ferret occupied and then selected random points within those colonies for each ferret, using a 5:1 ratio of the number of random points to each individual ferret's locations (Buskirk and Millspaugh 2006; Cooper and Millspaugh 1999). Because the study area was much larger than an individual ferret's activity area, we included a higher number of random points than at the activity-area scale to ensure adequate coverage of the area (Buskirk and Millspaugh 2006). For the perch analysis we calculated for each individual the percentage of ferret and random locations found within the 90-m buffers of perches, comparing them with a paired *t*-test for each study site. For the linear-feature analysis we calculated for each individual the average feature density found within 100-m buffers of ferret and random locations, comparing them with a paired *t*-test for each study site. Because of our consideration of type II errors and our greater concern about committing an error of a false negative than an error of false discovery (Dayton 1998; Stewart-Oaten 1995), and the highly endangered status of ferrets and small sample sizes for some tests, the significance level was set at $\alpha = 0.10$ for all statistical tests, all of which were 2-tailed. Assumptions of normality were assessed with the use of histograms, box plots, and probability plots. Statistical tests for the habitat-selection analyses were conducted in SAS version 9.1 (SAS Institute Inc. 2004).

Results

Survival analyses.—The leading cause of mortality of ferrets was predation by great horned owls (9 total deaths)

Table 2.—Causes of mortalities of reintroduced black-footed ferrets (*Mustela nigripes*) in Conata Basin/Badlands, South Dakota, during the radiotelemetry period, 1996 and 1997.

	Agate	Burns Basin	Sage Creek	Totals
Total no. ferrets	25	18	36	79
Causes of death				
Great horned owl	7	2	0	9
Other raptor	0	1	1	2
Coyote	5	5	2	12
Badger	1	0	0	1
Unknown	0	1	1	2
Total mortalities	13	9	4	26

and coyotes (12 total deaths), with higher owl and coyote predation in Agate and Burns Basin than in Sage Creek (Table 2). Two-week postrelease survival of ferrets did not vary by sex; the model containing sex differences (Table 1, models 4 and 8) did not receive as much support from the data based on AIC_c as the model containing no sex differences (Table 1, models 3 and 5). The best model for survival of ferrets killed by great horned owls incorporated the buffer covariate (Table 1, model 1), with strong support implied by the high normalized Akaike weight (w_i = 0.758). The coefficient of the buffer covariate in the best model did not include 0 (−6.71 ± 1.75 *SE*; 90% *CI* = −9.59, −3.84), suggesting that it was an important predictor of ferret survival. The probability of survival of ferrets decreased as the percentage of ferret locations inside the buffers of perches increased (Fig. 2). Exposure to the perch buffers was lower in Sage Creek than in Agate and Burns Basin (Fig. 3), consistent with the relatively high levels of owl predation at Agate and Burns Basin (Table 2). The model incorporating the distance to perch covariate (Table 1, model 2) also had some support (coefficient 0.01 ± 0.004 *SE*; 90% *CI* = 0.004, 0.016), with a ΔAIC_c of slightly >2 and weight of 0.238. The simpler model

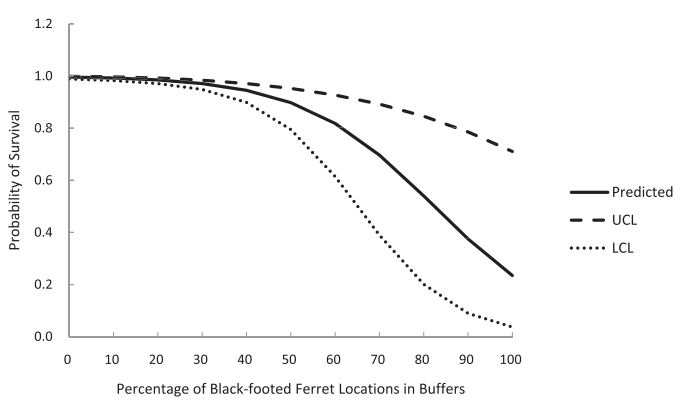

Fig. 2.—Probability of survival of reintroduced black-footed ferrets (*Mustela nigripes*) with respect to predation by great horned owls (*Bubo virginianus*) in Conata Basin/Badlands, South Dakota, 1996 and 1997, as a function of the percentage of ferret locations inside 90-m buffers of likely owl perches, based on the survival equation for the best model in program MARK. UCL = 90% upper confidence limit; LCL = 90% lower confidence limit.

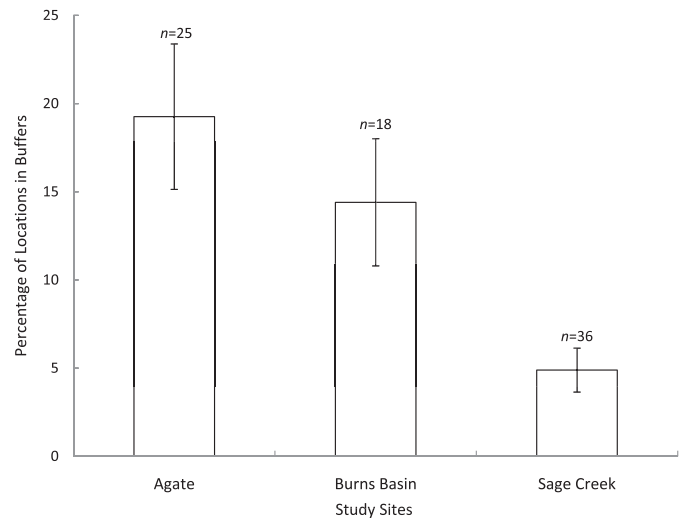

Fig. 3.—Mean (± *SE*) percentages of reintroduced black-footed ferret (*Mustela nigripes*) locations located within 90-m buffers of potential great horned owl (*Bubo virginianus*) perches at 3 study sites within Conata Basin/Badlands, South Dakota, 1996 and 1997. Larger percentages indicate higher predation exposure. Sample sizes (*n*) represent numbers of individual ferrets.

excluding a perch variable (Table 1, model 3) had little support (ΔAIC_c >10).

The best model for survival of ferrets killed by coyotes did not incorporate any of the covariates (Table 1, model 5), suggesting that the linear-feature covariates had little predictive value. The 2nd best model included the buffer covariate (Table 1, model 6); although the ΔAIC_c value was slightly <2, the coefficient of the covariate included 0 (94.80 ± 199.53 *SE*; 90% *CI* = −233.42, 423.03). Likewise, the coefficient of the covariate in model 7 (Table 1), incorporating distance to linear features, also included 0 (0.002 ± 0.007 *SE*; 90% *CI* = −0.009, 0.014). Hence, neither of these models were important predictors of ferret survival. The models containing the electric-fence covariate also had relatively little support (Table 1); the coefficient of the covariate in model 9 included 0 (0.075 ± 1.184 *SE*; 90% *CI* = −1.873, 2.023), whereas models 10 and 11 had considerably less support, with ΔAIC_c approaching 4.

Habitat-selection analyses.—In ferret activity areas ferret locations in Agate/Burns Basin were found within 90 m of potential owl perches significantly more than were random locations (t_{42} = 2.08, P = 0.04; Fig. 4a). Similarly, at the study-area scale ferret locations in Agate/Burns Basin were found within 90 m of perches significantly more than were random locations distributed throughout prairie dog colonies on which each ferret occurred (t_{42} = 2.61, P = 0.01; Fig. 4b). In contrast, percentages of ferret locations within 90 m of perches in Sage Creek were similar to the percentages of random locations at both the activity-area scale (t_{35} = 1.20, P = 0.24; Fig. 4a) and the study-area scale (t_{35} = −0.25, P = 0.80; Fig. 4b). Average densities of linear features potentially used by coyotes within the buffers of ferret locations at the activity-area scale were similar to random locations in Agate/

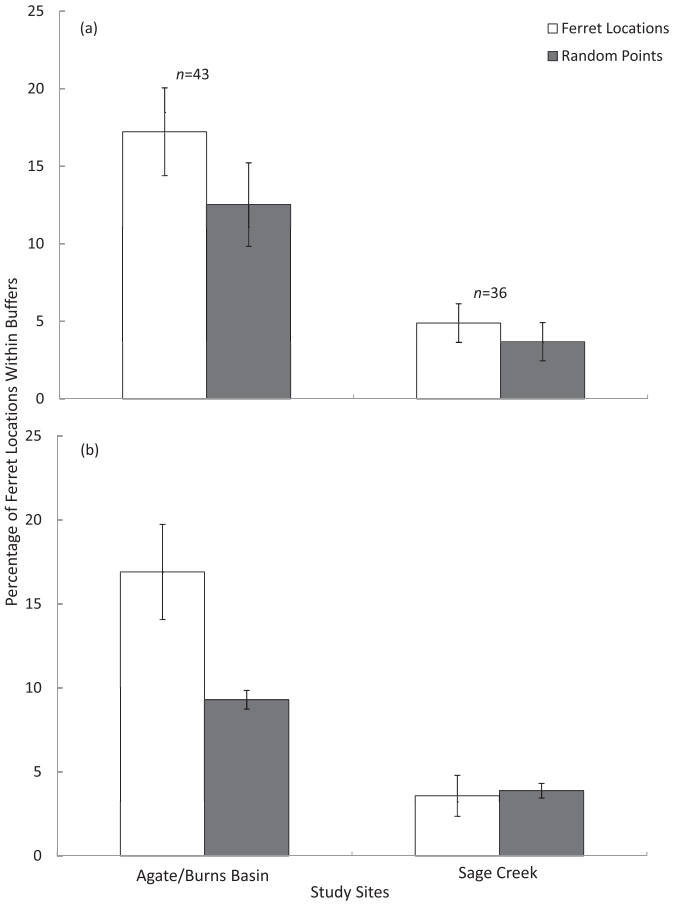

Fig. 4.—Mean (± *SE*) percentages of reintroduced black-footed ferret (*Mustela nigripes*) locations and random locations located within 90-m buffers of potential great horned owl (*Bubo virginianus*) perches and distributed throughout a) each ferret's activity area and b) prairie dog (*Cynomys ludovicianus*) colonies on which each ferret occurred at study sites within Conata Basin/Badlands, South Dakota, 1996 and 1997. Sample sizes (*n*) represent numbers of individual ferrets.

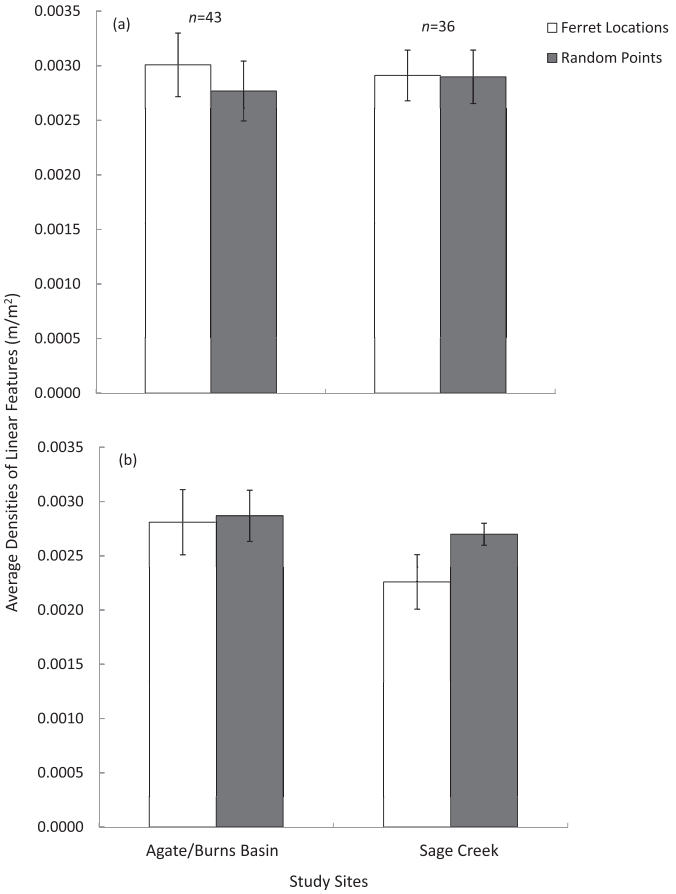

Fig. 5.—Mean (± *SE*) densities of linear features predicted to model coyote (*Canis latrans*) movement within 100-m buffers of reintroduced black-footed ferret (*Mustela nigripes*) locations and random locations distributed throughout a) each ferret's activity area and b) prairie dog (*Cynomys ludovicianus*) colonies on which each ferret occurred at study sites in Conata Basin/Badlands, South Dakota, 1996 and 1997. Sample sizes (*n*) represent numbers of individual ferrets.

Burns Basin ($t_{42} = 0.97$, $P = 0.34$; Fig. 5a) and Sage Creek ($t_{35} = 0.05$, $P = 0.96$; Fig. 5a), results that were repeated at the study-area scale for Agate/Burns Basin ($t_{42} = -0.20$, $P = 0.84$; Fig. 5b) and Sage Creek ($t_{35} = -1.49$, $P = 0.14$; Fig. 5b).

Discussion

Using easily quantifiable landscape features, we demonstrated that survival of reintroduced ferrets was significantly affected by exposure to perches likely used by great horned owls but not landscape features that might facilitate (i.e., potential movement routes) or deter (i.e., fencing) movement of coyotes. Both the activity level of a ferret within 90 m of a perch and average distance of a ferret from a perch were important predictors of ferret survival. Survival of ferrets decreased as the percentage of their total locations inside 90 m of perches increased. Corresponding to relative owl predation, exposure to perches was higher in Agate and Burns Basin, where 9 total ferrets were killed by great horned owls, than in Sage Creek, where no ferrets were killed by owls. The locations of perches likely contributed to these differences between the 2 sites. Perches in Agate/Burns Basin ($n = 193$) were distributed throughout the prairie dog colonies, and 41 (21%) were located within colony boundaries. Perches in Sage Creek ($n = 132$) were primarily distributed on the edges of colonies, and only 15 (11%) were located within colony boundaries. Notably, 3 great horned owls were removed lethally from Agate/Burns Basin during our study to reduce predation on ferrets. Without such lethal control mortality of ferrets due to owls at this site likely would have been higher, which might have resulted in an even greater effect of perches on ferret survival. Because owls are nocturnal, hunt from perches, and view ferrets as prey, they pose a considerable predation threat to ferrets. Our results suggest that landscape features that might be used as perches by great horned owls serve as good predictors of predation risk for reintroduced ferrets.

Coyotes are one of the primary causes of ferret mortality, and in the Conata Basin/Badlands area they have displayed

nocturnal activity, with higher nighttime than daytime rates of movement (Schroeder 2007). Nonetheless, in contrast to predation risk from great horned owls, exposure of ferrets to linear landscape features predicted to be coyote movement routes had relatively little effect on ferret survival. The landscape features we chose to model might not have been used frequently by coyotes or, if they were, did not appear to influence ferret predation risk. Although linear features are easily identified and mapped, other landscape attributes might predict more reliably predation risk from coyotes. For example, swift foxes (*Vulpes velox*) avoided high grass and dense shrubs that increased predation risk from coyotes (Thompson and Gese 2007); such structural habitat variables might be identified more clearly by prey animals and be more suitable as predictors of predation risk. Moreover, different hunting strategies of coyotes and owls likely contributed to the contrasting effects of predicted landscape features on ferret survival. Great horned owls are obligate carnivores that hunt from stationary perches that can be identified easily (Houston et al. 1998), whereas coyotes are opportunistic omnivores that forage throughout the landscape (Arjo and Pletscher 2004; Carrera et al. 2007; Cepek 2004). Use of landscape features to model predation risk by predators that use a broad spectrum of hunting strategies might be more difficult than modeling predation risk of predators with more consistent hunting patterns.

We found only modest support that electric fencing was effective for protecting ferrets from coyotes, similar to the findings of another study (Breck et al. 2006). Although we were not certain of the precise locations of ferret mortalities and whether ferrets were killed by coyotes inside or outside of fences, 1 likely reason electric fencing did not dramatically enhance survival could be that fences failed to exclude coyotes totally. Although coyotes initially were removed from within the electric fences, the 107-cm-high fences, which were used at ferret reintroduction sites at the time, might not have been tall enough to prevent coyotes from jumping over them (Acorn and Dorrance 1998; Thompson 1979). Hence, although electric fencing had little effect on ferret survival in our study, additional research will be valuable in addressing questions regarding fence effectiveness for excluding coyotes.

Contrary to our predictions and despite the strong impact of great horned owls on survival, our results suggest that predation risk generated by potential owl perches did not influence habitat selection of reintroduced ferrets. The naïve juvenile ferrets in our study might not have developed sensitivity to predation risk over the short interval postrelease, although at least some ferret antipredator behaviors are innate and species-specific (Biggins 2000; Bolles 1970), and we thus had reason to believe that juvenile reintroduced ferrets might exhibit such behaviors. Nonetheless, we cannot preclude involvement of learning and risk assessment, and given more time, ferrets might have chosen activity areas farther from potential owl perches. Ferrets also could have selected habitat based on factors other than assessment of predation risk, particularly considering that risk assessment might not always be part of the repertoire of ferret behaviors (Biggins 2000). Instead, ferrets could be selecting habitat based on high densities of prairie dogs, their preferred prey, and active burrows (Biggins et al. 2006d; Jachowski 2007). If so, our findings of ferrets closer than random to perches in Agate/Burns Basin might imply that high densities of active prairie dog burrows also were located near perches, potentially because prairie dogs favor changes in vegetation caused by livestock grazing pressure near water sources (Licht and Sanchez 1993) where cottonwood trees, which are preferred owl perches, also are located.

Repatriations of ferrets into their historical natural habitat areas are essential to the successful recovery of the species. Predation is an important factor in the mortality of wild ferrets, and our results suggest that future decisions concerning the location of reintroduction sites should consider the location and distribution of landscape features potentially used by great horned owls. To reduce predation risk to ferrets, management and control of great horned owls, or even removal of perches, might be necessary before reintroducing ferrets to a site. Although our analyses used a buffer of 90 m around likely owl perches, further research is warranted to evaluate more fully the distance from perches at which ferrets are relatively safe from predation. Coyotes also contribute substantially to ferret mortality, but factors other than the landscape features measured in our study need to be considered when using strategies to mitigate coyote predation on ferrets. Considering the predation risk to ferrets before reintroduction, and developing and implementing strategies to reduce such risk, will assist resource managers in the continued conservation of this endangered species. Further, the results of our study can be used to improve management strategies for other threatened and endangered species that currently are being reintroduced and recovered in the wild.

Acknowledgments

We especially appreciate the efforts of dedicated staff members at the National Black-footed Ferret Conservation Center (Wyoming), the Louisville Zoological Gardens, and the Phoenix Zoo for providing the ferrets we released. We thank G. Plumb of the National Park Service and B. Perry and P. McDonald of the United States Forest Service for their invaluable contributions to the radiocollaring and tracking of ferrets. We are indebted to the many technicians who spent long nights radiotracking the released ferrets. We thank C. Burdett for geographic information system assistance and R. Scherer and G. White for statistical advice. We also thank W. D. Walter and J. Resnik for providing comments on this manuscript. This study was supported by Colorado State University, the Rocky Mountain Goat Foundation, the Hill Memorial Fellowship, and the Women in Natural Sciences Fellowship. Support for the radiotelemetry work was provided by the United States Geological Survey, the National Park Service, and the United States Forest Service.

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Special Feature Editor was Barbara H. Blake.