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Postbreeding resource selection by adult black-footed ferrets in the Conata Basin, South Dakota

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We investigated postbreeding resource selection by adult black-footed ferrets (*Mustela nigripes*) on a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin of South Dakota during 2007–2008. We used resource selection functions (RSFs) to evaluate relationships between numbers of ferret locations and numbers of prairie dog burrow openings (total or active), distances to colony edges, and connectivity of patches of burrow openings. In both years ferrets selected areas near edges of the prairie dog colony where active burrow openings were abundant. In the interior of the colony ferrets selected areas with low abundance of active burrow openings. At times, prairie dog productivity (i.e., pup abundance) might be greatest at colony edges often characterized by grasses; ferrets are likely to select areas where refuge and vulnerable prey are abundant. Ferrets could have used interior areas with few active burrow openings as corridors between edge areas with many active burrow openings. Also, in areas with few active burrow openings ferrets spend more time aboveground during movements and, thus, are likely to be more easily detected. These results complement previous studies demonstrating importance of refuge and prey in fine-scale resource selection by ferrets and provide insight into factors that might influence edge effects on ferret space use. Conservation and restoration of colonies with areas with high densities of burrow openings and prairie dogs, and corridors between such areas, are needed for continued recovery of the black-footed ferret. RSFs could complement coarse-scale habitat evaluations by providing finer-scale assessments of habitat for the black-footed ferret.

Key words: *Cynomys*, *Cynomys ludovicianus*, edge, habitat, *Mustela*, *Mustela nigripes*, prairie dog

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Resource selection involves behavioral responses by wildlife to environmental and physiological stimuli (Hilden 1965), resulting in disproportionate use of some resources relative to others (Johnson 1980). Animals often select resources in a manner that increases fitness (Martin 1998; Pulliam and Danielson 1991). Accordingly, investigation of resource selection aids in identification of resources contributing to, and perhaps required for, population and species persistence. Therefore, such investigation is important in conservation of endangered species, such as the black-footed ferret (*Mustela nigripes*).

Black-footed ferrets are dependent on prairie dogs (*Cynomys* spp.), colonial, burrowing sciurids. Ferrets prey almost exclusively on prairie dogs (≥90% of diet—Campbell et al. 1987; Sheets et al. 1972) and are reliant on prairie dog burrows for refuge and den sites (Biggins et al. 2006c; Forrest et al. 1988). Prairie dogs and black-footed ferrets were once abundant throughout the Great Plains of North America (Anderson et al. 1986; Hoogland 2006; Slobodchikoff et al. 2009). However, since the early 1900s prairie dog numbers have declined precipitously due to poisoning campaigns (Forrest and Luchsinger 2006), recreational shooting (Reeve and Vosburgh 2006), and the concurrent expansion of plague, an invasive zoonotic disease caused by the bacterium *Yersinia pestis*, to which prairie dogs and ferrets are highly susceptible (Biggins et al. 2010; Matchett et al. 2010). All species of *Cynomys* are now of conservation concern (Hoogland 2006, 2007; Slobodchikoff et al. 2009). Black-footed ferrets are

endangered and currently conserved via captive propagation and reintroductions (Biggins et al. 2011b; Marinari and Kreeger 2006; Miller et al. 1994a; United States Fish and Wildlife Service 2006; Williams et al. 1991).

Advances in ferret recovery continue (Biggins et al. 2011b; Lockhart et al. 2006); however, current population estimates suggest that reintroduction efforts have not met recovery goals (United States Fish and Wildlife Service 2006), except at a handful of sites. Although numerous factors might mediate species recovery (Biggins et al. 2011b; Biggins and Godbey 2003; Miller et al. 1996; Reading et al. 1996), it has been suggested that ''the most pressing limitation to ferret recovery is availability of suitable habitat to restore and support wild populations'' (Lockhart et al. 2006:15). Habitat evaluations for ferrets involve estimating coarse-scale abundance of prairie dogs and, subsequently, carrying capacities of complexes (colonies separated by $\leq$7 km—Biggins et al. 1993) and subcomplexes ($\leq$1.5 km between colonies—Biggins et al. 2006d). Reintroductions then are prioritized by site, under additional consideration of disease and management conditions (Jachowski and Lockhart 2009). Continued decline in prairie dog abundance (Hoogland 2006, 2007; Slobodchikoff et al. 2009) limits recovery success and increases the relevance of identifying sites suitable for ferret reintroduction.

Resource selection function (RSF) models estimate species response to resources and can be used to estimate the probability of species occurrence (Johnson et al. 2004; Manly et al. 2002; Scott et al. 2002). RSFs could be used to project the relative predicted occurrence of black-footed ferrets in individual prairie dog colonies. Managers then could further prioritize restoration and conservation of prairie dog habitat and reintroductions and translocations of ferrets (e.g., Biggins et al. 2011a).

Although numerous resources might mediate habitat suitability for black-footed ferrets, previous studies of ferrets and other *Mustela* species implicate particular importance of prey and refuge densities, habitat connectivity, and edge effects. Densities and distributions of prey and refuge influence space use by many *Mustela* species (Erlinge and Sandell 1986; Fagerstone 1987; King and Powell 2007). Prairie dogs and the burrows (i.e., refuges) they construct are heterogeneously distributed in colonies (Biggins et al. 2006c; Hoogland 1995; Jachowski et al. 2008). Individual ferrets have been observed to concentrate space use in areas where burrow openings are abundant (Biggins et al. 1985, 2006c; Richardson et al. 1987), particularly where active burrow openings (fresh prairie dog feces) are relatively abundant (Jachowski 2007; Livieri 2007). Habitat connectivity (Crooks and Sanjayan 2006; Taylor et al. 1993; With et al. 1997) and edge effects (Leopold 1933; Wiens 1976) have long been implicated as mediating wildlife–habitat relationships in general and appear to influence the spatial ecology of at least some *Mustela* species (e.g., long-tailed weasels [*M. frenata*]—Gehring and Swihart 2004). Colony edges influenced resource selection by ferrets, albeit variably, on a black-tailed prairie dog (*C. ludovicianus*, hereafter prairie dog) colony in South Dakota; some ferrets appeared to select areas near colony edges, whereas other ferrets did not (Jachowski 2007). Regarding habitat connectivity, in South Dakota ferrets selected prairie dog colonies in close proximity to other colonies, particularly large colonies (Livieri 2007).

The aforementioned studies of ferret resource selection have concentrated on space use by individual ferrets in distinct colonies (Biggins et al. 2006c; Jachowski 2007; Livieri 2007) or among colonies in a prairie dog complex (Livieri 2007). An investigation of factors contributing to variable edge effects, reported by Jachowski (2007), is needed. Also, influences of habitat connectivity at within-colony scales (e.g., patches of burrow openings) have not been addressed for the black-footed ferret but would complement the investigation by Livieri (2007) of resource selection among colonies.

We investigated postbreeding resource selection by adult black-footed ferrets inhabiting a prairie dog colony in South Dakota during 2007–2008. Our main objective was to develop predictive models of ferret occurrence in prairie dog colonies. We developed RSFs to evaluate the potential influences of density of prairie dog burrow openings, density of active prairie dog burrow openings, prairie dog colony edges, and connectivity of patches of burrow openings on resource selection by ferrets to increase knowledge of the ecology of this endangered carnivore.

Materials and Methods

Study site.—We conducted our study on a 452-ha prairie dog colony (North American Datum 1927 Universal Transverse Mercator: 13N N4848099, E716705) of the Conata Basin ($\sim$29,000 ha), a northern mixed-grass prairie site in southwestern South Dakota classified as an ''experimental and non-essential'' recovery area under section 10(j) of the Endangered Species Act (United States Fish and Wildlife Service 2006). The study colony, inhabited by ferrets of captive ancestry since reintroductions in 1997 (Livieri 2006), is on land administered by the United States Department of Agriculture Forest Service (Buffalo Gap National Grassland). In designated periods cattle grazed within the colony. The colony is bordered by badland buttes and seasonal water drainages of variable depths, except for the northern tip, which extends into Badlands National Park (United States Department of Interior, National Park Service). We used the equation of Biggins et al. (1993) to estimate prairie dog density at 41.03 individuals/ha in 2007. Predominant vegetation includes western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), and buffalo grass (*Buchloe dactyloides*), along with mixed forbs in heavily grazed areas.

Burrow opening and colony mapping.—During July through mid-September 2007, the period of greatest prairie dog abundance and activity (Hoogland 1995), we recorded the locations of prairie dog burrow openings using Trimble CMT MC-V global positioning system receivers (Trimble Navigation Limited, Sunnyvale, California) mounted on all-terrain

vehicles (Jachowski et al. 2008). We classified burrow openings (sensu Biggins et al. 1993) as active (n = 58,633), inactive (n = 6,753), or plugged (n = 2,527). To limit remapping we adhered to rows delineated by fluorescent flags and marked the edge of mapped burrow openings with DeltaDust (Bayer Environmental Science, Durham, North Carolina), a deltamethrin-based pyrethroid used in flea control to halt the spread of plague (Seery et al. 2003). Differential correction ranged from 99% to 100%; we assumed location error $\leq$ 1 m (Jachowski et al. 2010). Proportionate activity of burrow openings was the same in 2007 and 2008 in 92.2% (i.e., 177) of 192 circular plots (20-m radius) distributed throughout the study colony (D. A. Eads, pers. obs.).

Prairie dog colony boundaries can be delineated in many ways (Biggins et al. 2006e). Ferrets often limit nondispersal movements to areas with prairie dog burrows (Biggins et al. 1985, 2006c). At fine scales ferrets are likely to perceive an area in which burrows are nonexistent to be a habitat edge. Therefore, in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California) we buffered all burrow openings by 20-m-radius circle polygons and dissolved these polygons to create a 20-m colony buffer. We contracted this buffer by 20 m to create a colony boundary; the colony thus excluded areas > 20 m from the nearest mapped burrow opening (Fig. 1). We assumed constancy of this boundary between 2007 and 2008.

Black-footed ferret spotlight surveys.—We monitored black-footed ferrets during spotlight surveys (Biggins et al. 2006b; Campbell et al. 1985; Clark et al. 1984). Each year in July–August we trapped ferrets during 1 or more 3- to 4-night periods (Biggins et al. 2006b). Reobservation data on marked ferrets suggested that we monitored all adult ferrets that resided on the study colony each year. Five ferrets were present in both 2007 and 2008. For each of these ferrets area of occupancy (at fine scales) and identity of neighboring ferrets varied between 2007 and 2008.

On nearly consecutive nights, we concentrated surveys between 0000 and 0600 h, the period of greatest aboveground activity by ferrets (Biggins 2000; Biggins et al. 1986, 2011c; Clark et al. 1986). We established a survey route that maximized coverage of the colony while minimizing overlap. One observer conducted surveys using a field vehicle, mounted with a high-intensity 240 BLITZ Lightforce spotlight (http://www.lightforce.net.au/). The observer drove the vehicle 8–16 km/h and, under continuous illumination, maneuvered the spotlight beam to detect the emerald green eyeshine of ferrets (Biggins et al. 2006b). We limited disturbance (Campbell et al. 1985) by exposing ferrets to the minimum light required to identify the occupied burrow opening.

We marked most ferrets with uniquely numbered passive integrator transponders (AVID Microchip I.D. Systems, Folsom, Louisiana) and identified passive integrator transponder–marked individuals using automated readers (Biggins et al. 2006b; Fagerstone and Johns 1987). The loop antenna of a reader was placed over an occupied burrow opening; as the ferret emerged near or through the antenna, passive integrator transponder numbers were automatically recorded. We identified ferrets without passive integrator transponders via unique dye markings applied by trained personnel in mid-June of each year (Jachowski et al. 2010). Thus, all ferrets were individually identifiable. Research was completed under University of Missouri Animal Use and Care Committee Protocol 6839, and met guidelines of the American Society of Mammalogists for the use of mammals in research (Gannon et al. 2007).

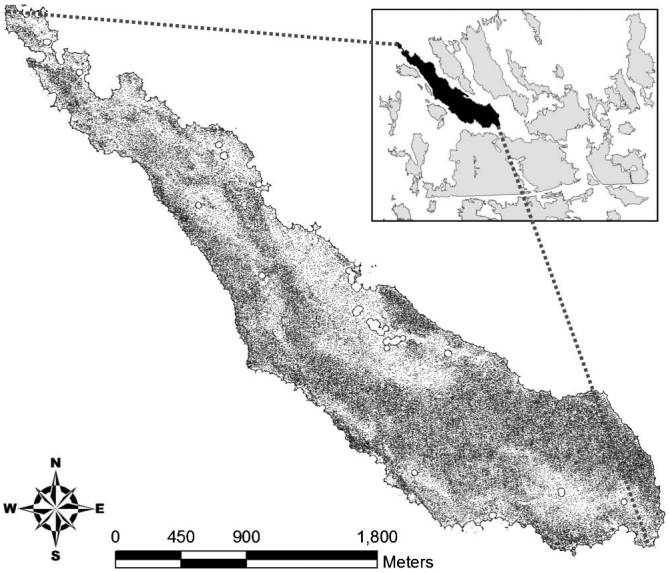

Fig. 1.—Spatial distribution of black-tailed prairie dog (*Cynomys ludovicianus*) burrow openings in a 452-ha colony in the Conata Basin (inset map), South Dakota. Density of dot-stippling indicates density of burrow openings; lines indicate the colony edge. We monitored space use by 21 adult black-footed ferrets (*Mustela nigripes*) inhabiting the colony (5 monitored during both years), 13 June–10 October 2007 and 11 June–27 September 2008.

We collected Universal Transverse Mercator coordinates of observation locations using handheld Garmin GPS 12XL Personal Navigator units (error $\leq$ 15 m; Garmin International, Inc., Olathe, Kansas). We included consecutive, confirmed locations of individual ferrets separated by $\geq$12 h in analyses (Livieri 2007); 88% of consecutive locations of individual ferrets were separated by $\geq$24 h.

Data analyses.—We developed RSFs by relating counts of ferret locations to resource attributes within a colony-wide grid system. We used an 80 × 80-m grid system. This grid-cell size reduced spatial autocorrelation of resources in grid cells (Eads 2009), thus identifying the scale at which resources were independent and reducing the likelihood of type I error (Hurlbert 1984). We related cell-specific counts of ferret locations to cell-specific resource attributes, including numbers of burrow openings, distance to colony edge, and connectivity of patches of burrow openings, variables suggested as important for ferrets or other *Mustela* species. We counted the number of burrow openings per cell; this count was separated into 2 numbers (inactive + active [i.e., total] and active). Plugged burrow openings were excluded. We calculated the Euclidean distance from the center of each

cell to the nearest colony edge. We also assigned each cell 2 connectivity scores. We categorized cells according to 5-level, ordered factors based on quantiles of 2 counts: the total number of burrow openings and the number of active burrow openings. Quantile classification grouped grid cells into 5 categories of equal numbers of cells. This delineated patches of cells of similar or dissimilar quantile values; these values did not serve as resource attributes but aided in calculating a connectivity index for numbers of burrow openings among neighboring cells. We calculated connectivity indices (FRAGSTATS—McGarigal et al. 2002) for each cell using:

$$\frac{\left(\frac{\sum_{r=1}^{Z} c_{ijr}}{a_{ij}}\right) - 1}{v - 1},$$

where c is the contiguity value for cell r in patch ij, a is the area of patch ij, and v is the sum of quantile values in the focal and neighboring ($n = 8$) cells. Connectivity values ranged from 0 (different values in all 8 cells) to 1 (equal values in all 8 cells). We weighted cell-specific connectivity values by corresponding numbers of burrow openings (total or active); increasing scores indicated increasing cell connectivity and density of burrow openings.

We used negative binomial regression, a type of generalized linear model with a log-link function and negative binomial error term (McCullagh and Nelder 1989), to fit year-specific models of ferret resource selection. Negative binomial regression is appropriate when analyzing overdispersed count data (Hilbe 2007), which was present in both years. Because of overdispersion, we used the log of the total number of ferret observations as an offset variable. We used a manual, forward model selection procedure to determine which predictor variables to include in main-effect(s) models. We 1st evaluated all single-parameter models and retained the variable with the lowest Akaike information criterion corrected for small sample size (AIC_c) value (Burnham and Anderson 2002). We created a 2-variable model by retaining the variable from the most highly supported 1-variable model and adding remaining variables separately. We retained the 2-variable model with the lowest AIC_c value. We added additional higher-order models in the same manner until a deviance ratio test (McCullagh and Nelder 1989) was no longer significant ($\alpha \geq 0.10$) or multiple models were supported (i.e., $\Delta AIC_c < 3.0$ with the added variable). The 2007 and 2008 models each contained 2 variables; we checked for interactions of the main effects. We assessed the fit of models with interactions, relative to main-effects models, using deviance ratio tests (McCullagh and Nelder 1989), retaining interactions if the test was significant. For each RSF we corrected for overdispersion by inflating coefficient standard errors by the square root of an overdispersion factor, derived as the sum of squared deviance residuals divided by the residual degrees of freedom (McCullagh and Nelder 1989).

We evaluated the predictive capabilities of year-specific RSFs using k-fold cross-validation (Boyce et al. 2002). We did not adjust frequencies of predicted RSF values by area (Boyce et al. 2002), because grid cells were of equal area. We divided grid-cell data into 5 random subsets. Each of these subsets comprised a training set (80% of cells) and a testing set (20% of cells). We iteratively withheld 1 of the 5 subsets, fit the regression model using the respective training data, and used estimated coefficients to predict values for the training and testing data sets. We separated predicted values into 32 equal-interval bins, scaled between the minimum and maximum values. When the predicted values of consecutive bins were 0 (i.e., when ferrets were predicted to be absent), we simplified the 32 bins to those bins with values >0. Using a Spearman rank correlation (r_s), we compared the frequencies, by bin, of predicted values for the test data of each model to the frequencies, by bin, of predicted values for the training data of respective models.

Results

During our study we monitored 21 unique adult ferrets (14 females and 7 males), 5 of which (4 females and 1 male) were present in 2007 and 2008. Between 13 June and 10 October 2007 (for 9 females and 3 males) and 11 June and 27 September 2008 (for 9 females and 5 males) we collected 458 ($\bar{X} = 38.2$, $SE = 2.7$, range = 12–47) and 418 ($\bar{X} = 29.9$, $SE = 3.9$, range = 2–55) observations of adult ferrets, respectively (Fig. 2). On average, we located individual ferrets during 41.04% of surveys in 2007 ($SE = 2.87\%$, range = 12.90–50.54%) and 35.13% of surveys in 2008 ($SE = 4.57\%$, range = 2.35–64.71%). The average number of total burrow openings per grid cell was 83.9 ($SE = 1.8$; range = 1–216). The average number of active burrow openings per grid cell was 75.3 ($SE = 1.6$, range = 0–190). Average distance of cell centers to the nearest colony edge was 130.72 m ($SE = 3.98$ m, range = 0–479.13 m).

The 2007 RSF, selected via the forward manual procedure, included 2 variables, the number of active burrow openings and distance to colony edge, and a significant ($\chi^2_1 = 6.532$, $P = 0.011$) interaction (Active burrow opening × Edge). Near colony edges ferrets selected areas with high densities of active burrow openings (Table 1; Fig. 3). In the colony interior ferrets appeared to select areas with a lower density of active burrow openings (Table 1; Fig. 3). Cross-validation indicated good model performance for all k-fold sets (all $r \geq 0.926$ and $P < 0.0001$). A similar pattern was found in 2008 (Table 1; Active burrow opening × Edge: $\chi^2_1 = 2.701$, $P = 0.100$). Cross-validation of the 2008 RSF indicated good model performance for all k-fold sets (all $r_s \geq 0.924$ and $P \leq 0.0001$).

Discussion

Black-footed ferrets selected areas where active prairie dog burrow openings were relatively abundant, namely near colony edges. These results corroborate previous research in the Conata Basin; individual ferrets concentrated space use in

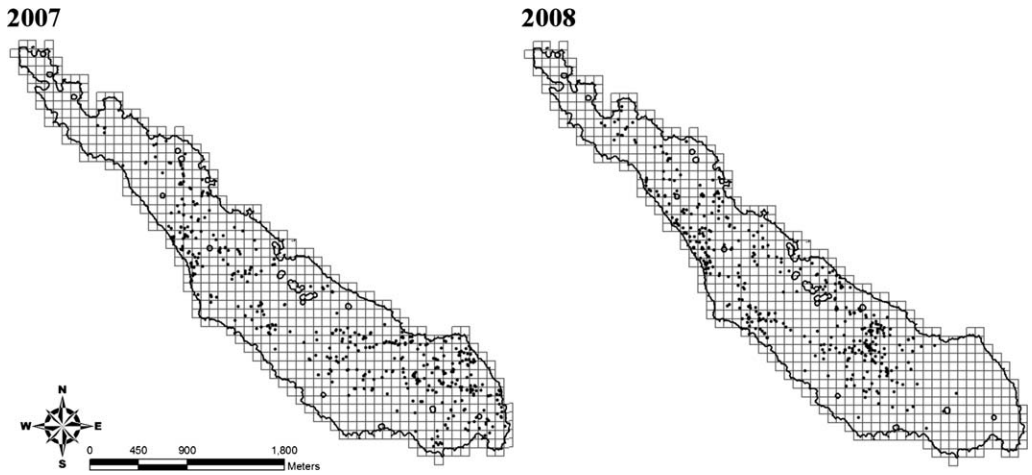

Fig. 2.—Spotlight observation locations (black dots) of adult black-footed ferrets (*Mustela nigripes*) in a system of 80 × 80-m grid cells overlain on a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony (Fig. 1) in the Conata Basin, South Dakota. We investigated postbreeding resource selection by 21 adult ferrets (5 monitored during both years), 13 June–10 October 2007 (n = 12 ferrets) and 11 June–27 September 2008 (n = 14 ferrets).

areas with high densities of active burrow openings (Jachowski 2007; Livieri 2007) where prairie dogs are often relatively abundant (Biggins et al. 1993, 2006d, 2006e; Johnson and Collinge 2004). Numerous predators (Hassell 1978), including many *Mustela* species, concentrate space use where prey are relatively abundant (*M. putorius* [Danilov and Rusakov 1969], *M. putorius furo* [Norbury et al. 1998], *M. erminea* [Erlinge and Sandell 1986], *M. frenata* [Gehring and Swihart 2003, 2004], and *M. nivalis* [Klemola et al. 1999]). Because prairie dogs comprise ≥90% of the ferret's diet, the black-footed ferret likely benefits from areas with high densities of prairie dogs. These areas also provide ferrets with burrows for shelter from predators and inclement weather.

Ferrets might select areas where active burrow openings are abundant not only because prairie dogs and refuge are present but because prairie dog burrow construction and modification could be greatest in such areas, allowing for selection of characteristics of refuge and den sites. Excavations of prairie dog burrows exhibit structural heterogeneity (Verdolin et al. 2008) that might enhance selection. Black-footed ferrets, like some *Mustela* (King and Powell 2007), are killed by semifossorial predators (e.g., badgers [*Taxidea taxus*—Biggins et al. 2006a, 2011d]) and are sensitive to thermal stress (Harrington et al. 2006). Ferrets might select dens for their complexity, depth, or temperature, or a combination of these factors (Forrest et al. 1985; Harrington et al. 2006; Sheets et al. 1971). In Shirley Basin, Wyoming, ferrets selected white-tailed prairie dog (*C. leucurus*) burrow systems with multiple openings to the surface (D. E. Biggins, pers. obs.). The Siberian polecat (*M. eversmanii*—Stroganov 1969), a close relative of *M. nigripes* (O'Brien et al. 1989), and the short-tailed weasel (*M. erminea*—King and Powell 2007) also appear to select for characteristics of den sites (e.g., number and sizes of openings). Perhaps where prairie dog density is

Table 1.—Negative binomial postbreeding resource selection functions for black-footed ferrets (*Mustela nigripes*) on the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, South Dakota, 2007–2008. Parameters are listed with estimates (β), standard errors (*SE*), lower and upper Wald's 95% confidence intervals (95% *CI*), chi-square (χ^2) test statistics, and probability values (Pr > χ^2).

Variable	β	*SE*	Wald's 95% *CI* Lower	Wald's 95% *CI* Upper	χ^2	Pr > χ^2
2007						
Intercept	−9.3921	0.2531	−9.9888	−8.7953	951.66	<0.0001
Active burrow opening	0.0263	0.0026	0.0202	0.0324	71.24	<0.0001
Edge	0.0109	0.0018	0.0066	0.0152	24.65	<0.0001
Active burrow opening × Edge	−0.0001	0.0001	−0.0001	0.0000	18.21	<0.0001
Dispersion	1.5186	0.1918	1.0663	1.9709		
2008						
Intercept	−8.8321	0.2331	−9.3978	−8.2664	936.34	<0.0001
Active burrow opening	0.0199	0.0024	0.0140	0.0258	43.35	<0.0001
Edge	0.0092	0.0019	0.0047	0.0136	16.30	<0.0001
Active burrow opening × Edge	−0.0001	0.0001	−0.0001	0.0000	10.05	0.0015
Dispersion	2.1100	0.2496	1.5043	2.7158		

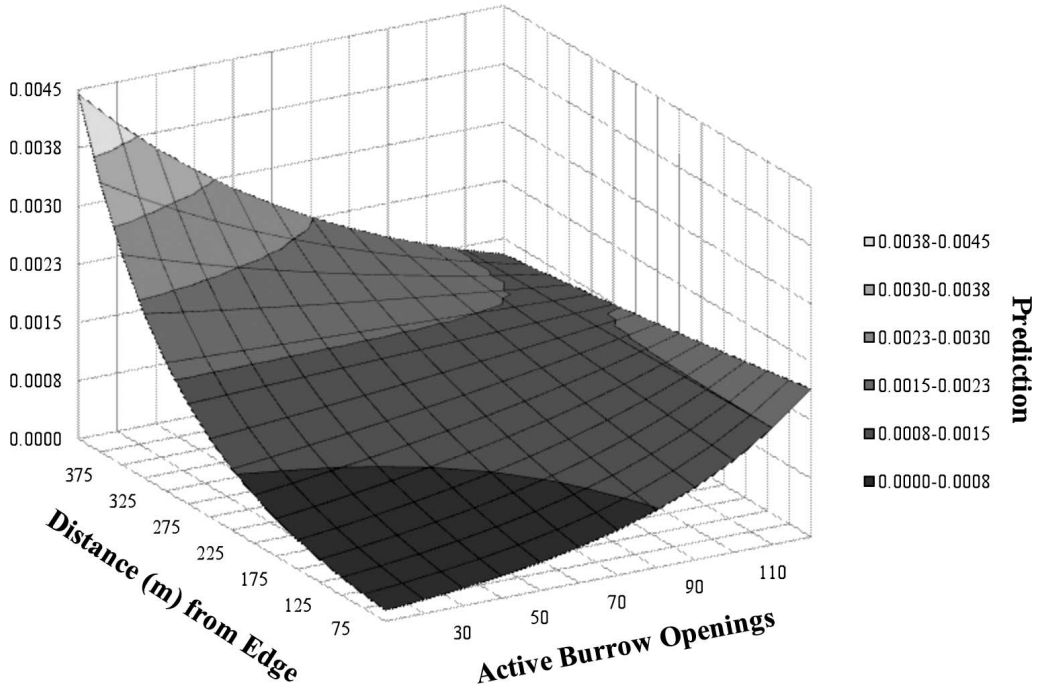

Fig. 3.—A 3-dimensional, predictive surface derived from the 2007 (13 June–10 October) black-footed ferret (*Mustela nigripes*) resource selection function (Table 1) that estimated influences of active black-tailed prairie dog (*Cynomys ludovicianus*) burrow opening counts in grid cells, euclidean distance from grid-cell centers to the nearest colony edge, and an interaction (Active burrow opening × Edge) upon predicted counts of ferret locations (Prediction) in the grid cells overlain on a 452-ha prairie dog colony in the Conata Basin, South Dakota.

high, ferrets most frequently find burrows with characteristics that facilitate predator avoidance and thermoregulation.

Colony edges appeared to influence resource selection by ferrets. The edge effects we observed were dependent on densities of active burrow openings (Active burrow opening × Edge interaction). If the density of active burrow openings was high near a colony edge, ferrets selected the area. Ferrets might use such edge areas to acquire prey but also as corridors to traverse colonies; where refuge is abundant, predation risk is reduced. In contrast, if the density of active burrow openings was low near a colony edge, ferrets rarely selected the area. In a previous study some ferrets apparently avoided colony edges, but some ferrets selected areas near colony edges (Jachowski 2007). Densities of active burrow openings vary among colony edges. Such variability of habitat structure at colony edges in areas occupied by different ferrets might explain why some ferrets select areas near colony edges and other ferrets do not.

Trophic interactions likely contribute to variability in prairie dog abundance at colony edges and could influence edge effects on ferret space use. At some colony edges in mixed-grass prairies vegetation often is characterized by mixed (e.g., *P. smithii*) and short (e.g., *B. gracilis* and *B. dactyloides*) grasses, species frequently consumed by prairie dogs (Fagerstone et al. 1981; Garrett et al. 1982; Lehmer et al. 2006; Summers and Linder 1978; Tileston and Lechleitner 1966; Uresk 1984). Where grasses are abundant, prairie dogs tend to be most abundant. For instance, on 2 colonies in Wind Cave National Park, South Dakota, densities of prairie dogs increased between 1985 and 1986 in edge areas characterized by grasses (Brizuela 1987). At sites where grasses are most abundant at colony edges, prairie dog pups are also most abundant. Earlier research in the Conata Basin suggested that female prairie dogs produced more pups in areas composed mainly of grasses (Cincotta 1985). Ferrets might frequent these areas if refuge density is sufficient; examination of recent data indicates that during the postbreeding season female ferrets selectively prey on prairie dog pups (D. E. Biggins and D. A. Eads, pers. obs.). If prairie dog pups are abundant in edge areas, prairie dog nests might also be abundant; ferrets might selectively den in prairie dog dens lined with grasses (Hoogland 1995; Sheets et al. 1971) that could insulate burrow systems (Gedeon et al. 2010).

Edge-associated costs, if they exist, are currently unclear for ferrets. We suspect costs of edges, like the aforementioned potential benefits, would vary spatially. Habitat characteristics, in addition to density of burrow openings and vegetation abundance, vary at the edges of prairie dog colonies. For instance, in the Conata Basin, some colony edges are near seasonal drainages, but others are not. These and other features (e.g., perch sites for birds of prey) near colony edges might influence space use by predators of ferrets, and perhaps predation risk for ferrets (Poessel et al. 2011).

In general, ferrets concentrate most activities in areas where active burrow openings are abundant. However, the RSFs suggested that in the interior of the study colony ferrets selected areas with low densities of active burrow openings. At least 3 factors could explain this result. First, ferrets might use areas with low abundance of active burrow openings as corridors between areas with high abundance of active burrow openings. Second, exploratory movements outside areas with

high abundance of burrow openings might have been most frequent when we monitored ferrets. In New Mexico ferrets used areas with low abundance of burrow openings after midnight (i.e., the primary period in which we monitored ferrets), relative to areas of use before midnight (Chipault 2010). Third, in addition to these nonexclusive behavioral phenomena, habitat-dependent detection could explain in part the apparent increased use by ferrets of interior areas with low abundance of active burrow openings. For instance, when in areas with low abundance of active burrow openings, ferrets might spend more time aboveground and, consequently, be more easily detected via spotlight surveys.

The ferret RSFs have limitations and require evaluation and validation within and outside the Conata Basin. Within the Conata Basin colonies differ in resource density and distribution (D. A. Eads, pers. obs.), and thus ferrets might behave differently on different Conata Basin colonies. At prairie dog sites outside the Conata Basin densities of burrow openings differ (Jachowski et al. 2008), and inactive burrow openings might be more or less common (86% of burrow openings were active at our study colony). Thus, at sites outside the Conata Basin ferrets might use space and select resources differently. For instance, at sites where the activity of burrow openings is lower, ferrets might use more frequently areas where inactive burrow openings are abundant, perhaps when moving between patches of active burrow openings. Also, burrow openings are more clustered at white-tailed than black-tailed prairie dog sites (D. A. Eads, pers. obs.). Thus, at white-tailed prairie dog sites, in particular, connectivity of patches of burrow openings might influence ferret resource selection; that is, although we found no support for an influence of habitat connectivity on ferret resource selection, habitat connectivity might be important to ferrets at other sites or scales of assessment. In addition to influences of habitat structure upon RSF performance, ferret resource selection likely varies by season (e.g., breeding season or postbreeding season). Future RSFs could evaluate these hypotheses, and a suite of RSFs could be used to predict how ferrets respond to the variable habitats created and maintained by prairie dogs, the principal prey of the black-footed ferret.

Conservation and management implications.—At the Conata Basin black-footed ferrets selected areas with high densities of burrow openings (inactive + active) and active burrow openings (Biggins et al. 2006c; Jachowski 2007; Livieri 2007). Female ferrets seem to produce more kits when inhabiting such areas (D. E. Biggins, pers. obs.); thus conservation and restoration of colonies with high densities of burrow openings and prairie dogs are needed to promote continued recovery of the black-footed ferret. Such actions also would aid in conservation of prairie dogs, keystone species of the Great Plains (Kotliar 2000; Kotliar et al. 1999, 2006; Miller et al. 1994b), and additional associated species.

Ferrets also use areas with low abundance of active burrow openings, as indicated by our results. Thus, areas with low densities of active burrow openings, although of lower quality for ferrets relative to areas with high density of active burrow openings (i.e., those areas used most frequently by ferrets), should be conserved. Management practices then can be directed toward increasing prairie dog densities in all areas, thus increasing the number of burrows and prey potentially available to ferrets. For instance, restoration practices, including translocations (Long et al. 2006; Truett et al. 2006) and plague control (Seery et al. 2003), can be used to increase densities of prairie dogs and active burrow openings and thus facilitate ferret recovery. Such efforts also might benefit the large number of species that associate with prairie dogs, including species other than the black-footed ferret that also historically have declined in number (e.g., the mountain plover [*Charadrius montanus*—Knopf 1994] and the burrowing owl [*Athene cunicularia*—Desmond et al. 2000]).

Accumulating evidence, here and elsewhere (Biggins et al. 2006c; Jachowski 2007; Livieri 2007), regarding fine-scale resource selection by ferrets suggests utility in assessing the fine-scale distribution of burrow openings when evaluating potential black-footed ferret habitat. Current habitat evaluations (Biggins et al. 1993, 2006d) involve coarse-scale consideration of this variable. Resource selection models could complement evaluation procedures by providing a method of predicting ferret occurrence within colonies. Although a recent resource utilization function model (Jachowski 2007) performed satisfactorily under evaluation with independent data (Eads et al., in press), and our RSFs performed well under cross-validation, the models require ground mapping of prairie dog burrow openings, which might not be feasible when evaluating expansive sites (Eads 2009). A more efficient method of mapping burrow openings is needed (e.g., satellite imagery mapping—Addink et al. 2010). When such a method is developed, resource selection models could complement or supplant the coarse-scale approach to evaluating habitat for the black-footed ferret and aid in evaluating habitat at fine scales throughout the range of this endangered carnivore.

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