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ABSTRACT: The black-footed ferret (*Mustela nigripes*), once extinct in the wild, remains one of the most critically endangered mammals in North America despite 18 years of reintroduction attempts. Because black-footed ferrets are specialized predators of prairie dogs (*Cynomys* sp.), a better understanding of how black-footed ferrets select resources might provide insight into how best to identify and manage reintroduction sites. We monitored ferret resource selection at two reintroduction sites with different densities of prairie dog populations—one that contained a high density of prairie dogs (Conata Basin, South Dakota) and one that was lower (UL Bend, Montana). We evaluated support for hypotheses about ferret resource selection as related to the distribution of active burrows used by black-tailed prairie dogs (*Cynomys ludovicianus*), interactions between ferrets, and habitat edge effects. We found support for all three factors within both populations; however, they affected ferret resource selection differently at each site. Ferrets at Conata Basin tended to select areas with high prairie dog burrow density, closer to the colony edge, and that overlapped other ferret ranges. In contrast, ferrets at UL Bend tended not to select areas of high active prairie dog burrow density, avoided areas close to edge habitat, and females avoided areas occupied by other ferrets. The differences observed between the two sites might be best explained by prairie dog densities, which were higher at Conata Basin (119.3 active burrows per ha) than at UL Bend (44.4 active burrows per ha). Given the positive growth of ferret populations at Conata Basin, management that increases the density of prairie dogs might enhance ferret success within natural areas. To achieve long-term recovery of ferrets in the wild, conservationists should increasingly work across and outside natural area boundaries to increase prairie dog populations.

Index terms: black-footed ferret, black-tailed prairie dogs, Conata Basin, reintroduction, UL Bend

INTRODUCTION

Successful reintroduction of an endangered species relies on knowledge of its behavior and habitat requirements. A thorough understanding of wildlife-habitat associations is identified as a priority in reintroduction guidelines (IUCN 1998) and in review papers describing factors affecting translocation success (Beck et al. 1994; Wolf et al. 1996). For endangered species, careful site selection is particularly important because reintroduction sometimes is the only viable option for species recovery (Kleiman 1989; Van Wieren 2006). With carnivore reintroduction, the stakes often are high because of real or perceived human conflicts (Reading and Kellert 1993; Povilitis et al. 2006; Gusset et al. 2008), such as human safety or competition with human-valued resources, and the precarious status of some carnivores (Purvis 2000).

The black-footed ferret (*Mustela nigripes*, hereafter referred to as ferret) once was extinct in the wild and efforts to establish populations have had limited success. Only four of 18 reintroduction sites for the ferret have been successful at establishing self-sustaining populations for multiple years and fewer than 1000 individuals currently exist in the wild (Jachowski and Lockhart 2009). Disease is likely a major factor reducing ferret survival and prairie

dog (*Cynomys ludovicianus*) abundance at reintroduction sites (Matchett et al. 2010). However, at sites where ferret and prairie dog populations persist, we have a poor understanding of why ferret populations do not reach potential sizes predicted by current models.

A better understanding of how ferrets select resources might improve management and reintroduction success. Although we know ferrets occur only on prairie dog colonies (Biggins et al. 1985; Biggins et al. 2006b), we know little about their use patterns on these areas. Previous investigations of ferret habitat relationships focused on population-level assessments at relatively large spatial scales (e.g., the size and average burrow density of an entire prairie dog colony or complex) (Forrest et al. 1985; Miller et al. 1988; Biggins et al. 1993; Biggins et al. 2006c), but recent findings suggested that upon release, ferrets selected and competed for areas at much finer scales (Biggins et al. 2006b). Consequently, Biggins et al. (2006c) hypothesized that competition among individuals might limit the density and growth potential of ferret populations. Therefore, an evaluation of fine-scale resource selection by ferrets following their reintroduction might aid habitat assessments and recovery of the species.

In addition to prairie dogs, other factors, such as social interactions and predation risk, might affect fine-scale resource selection by ferrets. Because ferrets feed primarily on prairie dogs and rely on prairie dog burrow systems as den sites (Henderson et al. 1969; Sheets et al. 1972; Richardson et al. 1987), we first hypothesized that the density and distribution of burrows actively used by prairie dogs were important factors in ferret resource selection. Second, behavioral or social interactions between ferrets might affect ferret resource selection similar to other mustelid species (Johnson et al. 2000; Hellstedt and Henttonen 2006). Ferrets are polygamous and typically solitary, so male home ranges overlap the home ranges of multiple females, but overlap of home ranges among members of the same sex is less frequent (Biggins et al. 1985; Richardson et al. 1987). Therefore, we hypothesized that the social structure of ferrets influenced resource selection. Finally, predators can affect ferret survival (Forrest et al. 1988; Breck et al. 2006) and behavior (Miller et al. 1996). In particular, coyotes are major predators of ferrets (Biggins 2000). We hypothesized that the transition of short to tall vegetation associated with the edges of prairie dog colonies provides ambush cover for coyotes, leading ferrets to avoid such areas.

Our objectives were to assess resource selection of ferrets and to test the hypotheses noted above. We studied ferret resource selection at two reintroduction sites, including one site containing a high density of prairie dog burrows (Conata Basin, South Dakota) and one that was lower (UL Bend, Montana) (Jachowski et al. 2008).

METHODS

Study Areas

We selected study areas within two long-running reintroduction sites. We selected prairie dog colonies as study areas within these sites based on: (1) length of time since initial ferret reintroductions of at least five years (to more reasonably make the assumption that ferrets had time to establish spacing patterns) and (2) methodological and logistic limitations, such as accessibility and size of the colonies.

In 2006, all seven adult ferrets that were known to exist in the State of Montana occurred within UL Bend National Wildlife Refuge, which is managed as part of Charles M. Russell National Wildlife Refuge (U.S. Fish and Wildlife Service). Black-tailed prairie dog (*Cynomys ludovicianus*) colonies occupied 1120 ha at UL Bend. We selected the Locke sub-complex (525 ha) as our study area (Figure 1). It comprised approximately 47% of the entire reintroduction site. Ferrets were first reintroduced at the UL Bend site in 1994, with periodic augmentation until 2006 (Jachowski et al. 2008). During 2006, only seven ferrets were present at the site, and of those, four adult ferrets (three females and one male) were present in our study area.

The Conata Basin in southwestern South Dakota is a portion of Buffalo Gap National Grassland (U.S. Forest Service) where black-tailed prairie dog colonies occupied approximately 11,803 ha during our study (Livieri 2006). A total of 164 ferrets were reintroduced at the Conata Basin site between 1996-2000; and between 2000-2006, the site was estimated to have a self-sustaining population of > 200 individuals (Livieri 2006). We selected the North Enclosure prairie dog colony (201 ha) as our study area (Figure 1). This colony, one of the initial ferret reintroduction sites, has been inhabited by ferrets since 1997 and

without augmentation after 2000 (Livieri 2006; Jachowski et al. 2008). During both 2005 and 2006, six adult ferrets (four females and two males) were present in this study area.

Field Observations

We collected location data on all ferrets in our selected study areas on nearly consecutive nights from June through October in 2005 and 2006. Although various techniques can be used to locate and monitor ferret movements in the wild (Campbell et al. 1985), the most widely used technique for locating ferrets involves standardized, systematic spotlight surveys (Biggins et al. 2006a; Grenier et al. 2009). At each study area, we created a single survey route that provided nearly complete sampling coverage of the entire study area without overlap. We randomized our start times between dusk and 23:00 each night to ensure that we sampled locations along the route at different times each night.

We drove the survey routes using all-terrain or 4-wheel-drive vehicles with Lightforce® spotlights with a 1 million candlelight power rating. We drove vehicles between 8-16 kph with constant side-to-side scanning of the spotlight to detect ferret “eye shine.” We marked each adult ferret with a PIT (passive integrated transponder) implant (Fagerstone and Johns 1987) and

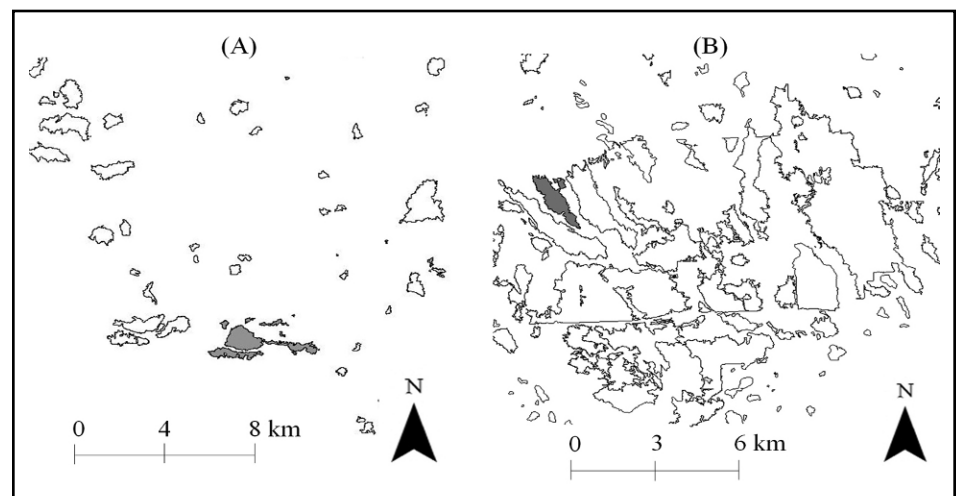


Figure 1. UL Bend, Montana (A) and Conata Basin, South Dakota (B) core black-footed ferret (*Mustela nigripes*) reintroduction sites, with polygons representing the maximum extent of burrow openings for individual colonies of black-tailed prairie dogs (*Cynomys ludovicianus*). Specific colonies included in this study are shaded grey.

with unique dye marks on the front and back of its neck (Grenier et al. 2009). Upon observing a ferret, we identified it by the dye marks or by placing a battery-operated ring PIT reader at the entrance of the burrow. We left the PIT reader at the burrow entrance, revealing its PIT identification number. We recorded the PIT number or the dye mark and obtained Universal Transverse Mercator (UTM) coordinates for the location of each observed ferret using hand-held, Garmin Global Positioning System 12XL Personal Navigator units that have an accuracy error < 7 m (Garmin International Inc., Olathe, Kan.). If we observed a ferret on multiple occasions in one night, as frequently occurred, we selected the first observation that was ≤ 24 hr after the previous observation to allow for one activity-period cycle and to limit serial autocorrelation between observations (Lair 1987; Minta 1990; Goodrich and

Buskirk 1998).

We mapped the distribution of prairie dog burrows within each study area to quantify the spatial distribution of prairie dogs within colonies and to identify colony boundaries. Prairie dog burrows correlate with the presence of prairie dogs, and are commonly used to examine the spatial distribution and abundance of prairie dogs (Uresk et al. 1982; Biggins et al. 1993; Johnson and Collinge 2004; Biggins et al. 2006d). Therefore, we used active prairie dog burrows as a surrogate for the spatial distribution of prairie dogs. We mapped locations of all prairie dog burrows at each study area in 2005 using teams of personnel trained in systematically locating prairie dog burrows and operating Trimble CMT MC-V GPS data loggers receivers (Trimble Navigation Limited, Sunnyvale, Calif.) mounted on all-terrain vehicles. We downloaded burrow location data and

differentially corrected locations using the nearest base station in GPS Pathfinder[®] Office 3.0 (Trimble Navigation Limited, Westminster, Colo.). We obtained correction rates of 99%-100% and, therefore, assumed burrow location error ≤ 1 m. During mapping, we classified burrows as either active or inactive based on presence of a prairie dog, prairie dog fecal material, or fresh digging (Dullum 2001).

Data Analysis

We used a resource utilization function (RUF) approach (Marzluff et al. 2004) to examine the relationship of space use by individual ferrets to resource attributes and behavioral interactions (Figure 2). We used the height of the ferret UD (utilization distribution) at each grid-point as the response variable in a multiple regression analysis where combinations of predictor

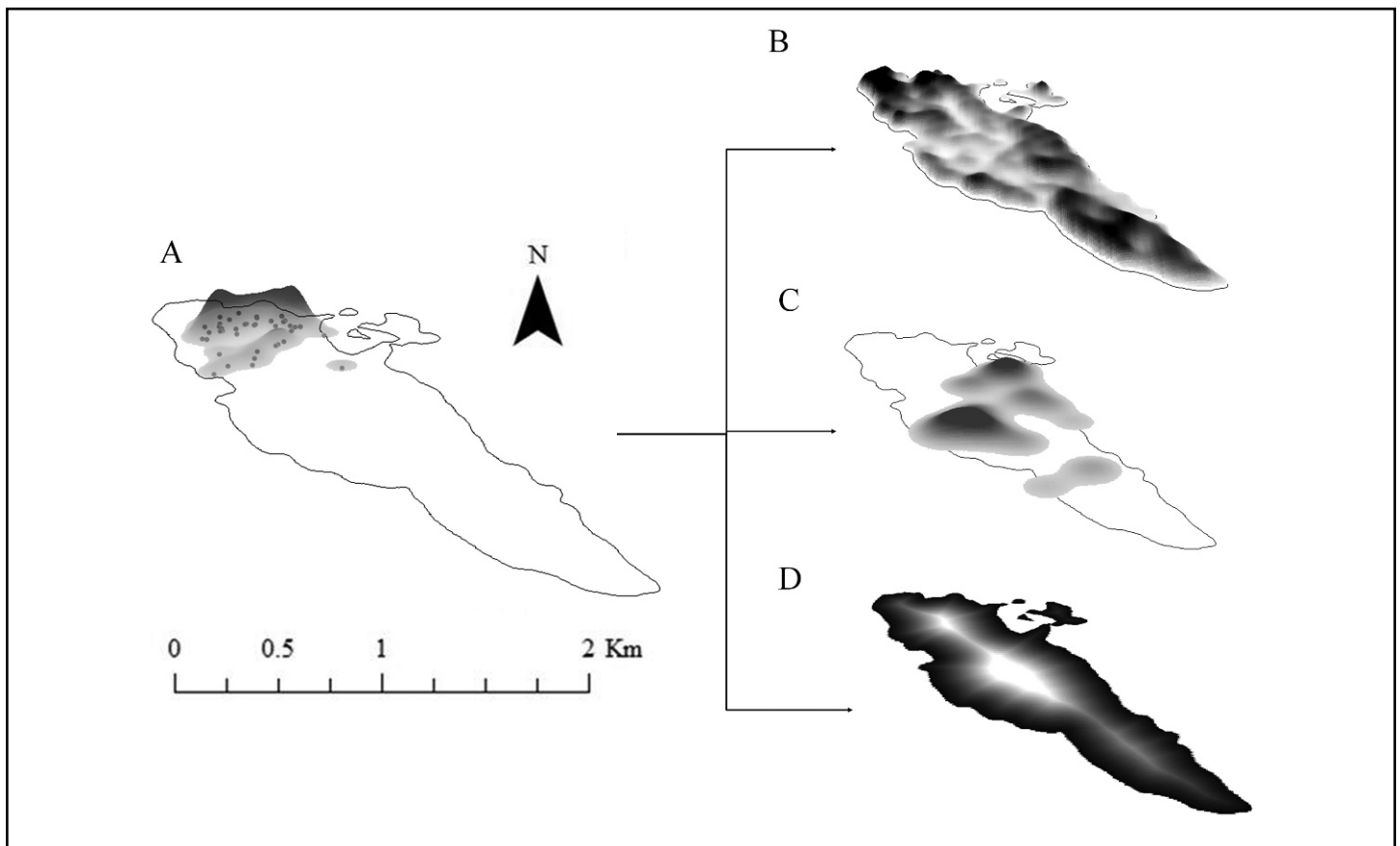


Figure 2. Calculation of a single resource utilization function for a female black-footed ferret (*Mustela nigripes*) within the Conata Basin black-tailed prairie dog (*Cynomys ludovicianus*) colony (depicted by a solid line) in 2005. First, observed locations of the ferret (solid dots) are used to estimate 95% fixed kernel utilization distribution (UD; inset A). Second, on a pixel-by-pixel basis UD values for the ferret are related to resource attributes through multiple regression techniques. We measured three types of resource attributes: (1) availability of active prairie dog burrows as measured through a UD (inset B); (2) overlap with and distance to the nearest male and female ferret (inset C); and (3) distance of the pixel to the edge of the colony (inset D) where darker areas represent locations close to the colony edge.

variables represented different hypotheses about ferret resource selection (Marzluff et al. 2004; Millsbaugh et al. 2006). Based on minimum recommended sample size criteria for calculating UD by Seaman et al. (1999), we only calculated a UD for individuals for which we were able to collect ≥ 30 observations within the 5-month sampling period. We developed 95% fixed kernels (Worton 1987; Worton 1989; Kernohan et al. 2001) to estimate UDs (van Winkle 1975) in Matlab (Mathworks Incorporated, Natick, Mass.) using the 'Kde folder' (Beardah and Baxter 1995) and "plug-in" methods for bandwidth selection (Wand and Jones 1995; Gitzen et al. 2006).

We developed 16 *a priori* models to evaluate three hypotheses that might affect ferret resource selection: distribution of active prairie dog burrows; space use interactions between ferrets; and predation risk associated with the proximity to the edge of the prairie dog colony (Table 1). We quantified the spatial distribution of prairie dog burrows across each study area (PDUD) by developing UDs of active prairie dog burrows based on burrow locations (Jachowski et al. 2008). We measured the spatial interaction between ferrets in two ways. First, we identified the peak activity area for each ferret by identifying the upper 5% by volume of the UD and then measured the distance from the edge of that peak activity area to the nearest male (PKML) and female (PKFL) peak activity area. Second, we assessed the potential effect of use intensity by other ferrets by measuring the UD values of the nearest male (TRML) and female (TRFL) ferret at each grid cell located within the area of space use overlap. Finally, to represent relative predation risk associated with the edge of prairie dog colonies (EDGE), we calculated Euclidian distance from the edge of the prairie dog colony (i.e., maximum extent of active prairie dog burrows) to all grid locations within the 95% UD of a ferret. We utilized Geographic Information System (GIS) to assign values of covariates at each ferret UD grid point in ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, Calif.).

We evaluated support for our models using

Akaike's Information Criteria (AIC) (Burnham and Anderson 2002). We assessed the support for each model for each ferret using ΔAIC and Akaike weights (w_i). Using the standardized RUF coefficients ($\hat{\beta}_j$) from the most supported model, we evaluated the relative importance of a specific resource attribute to resource selection for each individual ferret.

Although we developed our models at the level of an individual ferret to better understand individual variability across these habitat attributes (Figure 2), we also averaged individual models to generate a population level RUF for the ferret population at each study area (Marzluff et al. 2004; Millsbaugh et al. 2006). We examined standardized RUF coefficients ($\hat{\beta}_j$) from the most supported model for each ferret based on Akaike weights (Burnham and Anderson 2002). We estimated the population-level model coefficients of the most supported RUFs using

$$\hat{\beta}_i = \frac{1}{n} \sum_{j=1}^n \hat{\beta}_{ij}, \quad (1)$$

where $\hat{\beta}_{ij}$ is the estimate of coefficient i for individual j . The variance of the estimated population-level model coefficients was estimated using

$$Var(\hat{\beta}_i) = \frac{1}{n-1} \sum_{j=1}^n (\hat{\beta}_{ij} - \hat{\beta}_i)^2, \quad (2)$$

which includes both intra- and inter-animal variation (Marzluff et al. 2004). Last, we evaluated the predictive ability of our population-level RUFs using k -fold cross-validation for each population (Boyce et al. 2002).

RESULTS

We obtained > 30 locations within a field season for each of 16 adult ferrets ($\bar{x} = 44.8$, $SD = 11.5$, range = 32 - 71) present on our study areas (six in 2005 and six in 2006 at Conata Basin, and four at UL Bend in 2006). One male and two female ferrets were present during both years at Conata Basin; thus, we monitored a total of nine distinct individuals (six female and three male) over two years at that site. To avoid pseudoreplication when calculating

population-level metrics, we randomly selected and removed one year for each of the three ferrets present during both years (Hurlbert 1984). We did not locate animals a sufficient number of times (i.e., > 30 locations) in 2005 at UL Bend, but did in 2006. We used the single male at UL Bend in our analyses relative to the other ferrets, but did not assess resource selection for that individual because we could not evaluate its resource selection patterns in relation to another male.

The distribution of active prairie dog burrows, behavioral interaction metrics, and distance to the edge of the colony all influenced ferret resource selection. At the individual ferret level, the global model was either the most supported, or within 2 ΔAIC units for all animals. Therefore, we used the global model to calculate a population-level RUF for both study populations. We found further evidence of support for the global model through k -fold cross validation results for both ferret study populations, where the mean cross-validated Spearman-rank correlation values (r_s) for both populations were ≥ 0.9478 ($P < 0.0001$). Despite the consistency in global model support, the effects of individual parameters differed between our two study areas (Table 1).

At Conata Basin, the most important factors related to ferret resource selection were the positive influences of prairie dog active burrow UD value and the presence of other ferrets (Table 1). Seven of the nine ferrets (three males and four females) selected locations with greater prairie dog burrow density (Table 1). Eight of the nine ferrets (three males and five females) selected areas that also were occupied by the nearest female ferret (Table 1). Additionally, all nine ferrets at Conata Basin selected for locations that were occupied by the nearest male ferret. We failed to detect consistent selection or avoidance of areas in proximity to peak activity areas of other ferrets. Last, we observed mixed positive and negative effects of the distance to colony edge on ferret resource selection at Conata Basin (Table 1).

In contrast to Conata Basin, resource selection by ferrets at UL Bend was correlated

Table 1. Averaged population-level resource utilization coefficients (β) and standard errors (SE) and the direction (+ or -) and number of individuals related to resource covariates of black-footed ferrets (*Mustela nigripes*) at Conata Basin (n=9) and UL Bend (n=3).

Variable	Conata Basin			UL Bend		
	β (SE)	+	-	β (SE)	+	-
PDUD ¹	5.1 x 10 ⁻⁴ (7.5 x 10 ⁻⁷)	7	2	-9.4 x 10 ⁻⁴ (5.8 x 10 ⁻⁶)	2	1
EDGE ²	-3.0 x 10 ⁻⁴ (6.9 x 10 ⁻⁶)	4	5	1.3 x 10 ⁻³ (5.3 x 10 ⁻⁶)	3	0
PKFL ³	8.3 x 10 ⁻⁴ (2.2 x 10 ⁻⁵)	4	5	-6.2 x 10 ⁻⁴ (1.7 x 10 ⁻⁶)	1	2
PKML ⁴	-2.5 x 10 ⁻³ (4.1 x 10 ⁻⁵)	3	6	4.2 x 10 ⁻⁴ (1.0 x 10 ⁻⁶)	2	1
TRFL ⁵	1.8 x 10 ⁻³ (5.7 x 10 ⁻⁶)	8	1	-1.9 x 10 ⁻³ (5.0 x 10 ⁻⁶)	1	2
TRML ⁶	1.7 x 10 ⁻³ (2.6 x 10 ⁻⁶)	9	0	7.1 x 10 ⁻⁴ (9.8 x 10 ⁻⁷)	3	0

¹ Prairie dog burrow utilization distribution (UD) value within the cell

² Distance (m) to nearest edge of prairie dog colony

³ Distance (m) to nearest peak activity area for the nearest female ferret during that year

⁴ Distance (m) to nearest peak activity area for the nearest male ferret during that year

⁵ The UD value of the nearest female ferret at each grid cell located within the area of space use overlap

⁶ The UD value of the nearest male ferret at each grid cell located within the area of space use overlap

with areas away from other ferrets and with increasing distance from the edge of the prairie dog colony (Table 1). Ferret use of space at UL Bend generally decreased at locations with greater active prairie dog burrow density, although this result was not consistent among individuals (Table 1). Similar to Conata Basin, all female ferrets tended to select for areas near the peak activity area of the single male ferret.

DISCUSSION

The most striking result was the difference in the way prairie dog active burrow distribution influenced resource selection by ferrets at the two study sites. Prairie dog burrows were unevenly distributed across our study sites (Jachowski et al. 2008), and their distribution was the overriding factor influencing resource selection by ferrets at Conata Basin. This finding is not surprising because space use patterns by multiple carnivore species are primarily influenced by the distribution of prey (Eide et al. 2004; Cochrane et al. 2006),

including ferrets (Jachowski et al. 2010; Eads et al. 2011). In contrast, ferrets at UL Bend were more likely to use areas with lower active prairie dog burrow density. Similarly, at a reintroduction site in New Mexico, Chipault (2010) found that ferrets did not always select for areas of high prairie dog burrow density. These findings collectively suggest that while prey availability is important, other factors also might influence ferret resource selection patterns, particularly when prey density is low.

Behavioral or social interactions between ferrets influenced resource selection, but the influence of social interactions was tied to prey density. Male ferrets have been hypothesized to select for areas occupied by females and to be highly territorial towards other males (Richardson et al. 1987). While males at both study sites consistently selected for areas occupied by females during our study, at the Conata Basin, male ferret UD's overlapped extensively and additively encompassed

the entire study area (Jachowski 2007; Jachowski et al. 2010). This suggests that during the non-breeding or litter-rearing period (i.e., summer and fall), males either did not behave territorially towards other males but rather overlapped in the areas they occupied, or utilized similar areas spatially but temporally avoided each other. Female ferrets have been hypothesized to select and compete for (i.e., exclude other individuals from) areas of high prairie dog burrow density (Biggins et al. 2006b); however, this hypothesis was not fully supported at either site. Results from Conata Basin support the prevailing hypothesis that ferret space use generally is associated with higher prairie dog burrow density (Biggins et al. 2006b; Eads et al. 2011), but ferrets at Conata Basin also selected areas used by other ferrets. In contrast, ferrets at UL Bend were more likely to use areas with lower active prairie dog burrow density, and they did not select for areas frequented by other female ferrets. These results suggest more complex relationships between prey distribution

and social interactions of ferrets than has previously been hypothesized.

Given that the spatial distribution of critical resources was the primary influence on resource selection, and is generally acknowledged as such for solitary carnivores (Sandell 1989), the fine-scale differences in resource selection patterns that we observed within sites might be explained by larger-scale variation in habitat quality between sites. While we assessed resource selection in relation to the relative distribution of active prairie dog burrows within a site, the absolute density of burrows was nearly three times greater at Conata Basin (119.3 active burrows/ha) than at UL Bend (44.4 active burrows/ha) (Jachowski et al. 2008). Territoriality has been reported to occur only when there is a net benefit to defending quality areas of food resources (Carpenter and McMillen 1976; McLoughlin et al. 2000). Therefore, high prairie dog densities at Conata Basin might have negated the need to defend territories and, thus, facilitated overlap between ferrets. In contrast, ferrets at UL Bend appeared to defend discrete territories, suggesting that the density of prairie dogs at UL Bend was below a threshold at which female ferrets would tolerate space use overlap with other females.

Our findings support the use of predictive ferret population models that incorporate resource availability metrics and territorial interactions between ferrets. The size and quality of habitat has been shown to influence population size for a variety of carnivore species (Karanth et al. 2004; Hetherington and Gorman 2007). Early attempts to predict ferret population sizes at potential reintroduction sites focused on evaluating prairie dog populations based on large-scale metrics, such as the total area covered by a colony or average burrow density (Biggins et al. 1993). This predictive model then was used to rank reintroduction sites based on the total number of ferrets a site could maintain, where a site with the largest potential ferret population was typically the most highly ranked for reintroduction (Jachowski and Lockhart 2009). Our findings support the use of this predictive model. The site that contained a lower density of prairie dogs (UL Bend)

also contained ferrets that exhibited increased territorial behavior relative to the site containing higher prairie dog densities (Conata Basin). In addition, despite being over twice the size of the Conata Basin site, the UL Bend site contained less than half as many ferrets. Thus, we might expect reintroduction sites with low-density prairie dog populations to contain fewer ferrets than similarly sized areas with a higher density of prairie dogs.

Managers might be able to increase the number of ferrets within existing reintroduction sites by increasing the density of prairie dogs. Ferrets that use areas of high prairie dog burrow density have smaller home ranges and exhibit increased tolerance for space use overlap with other ferrets (Jachowski et al. 2010). We encourage managers to use management practices that enhance prairie dog density such as flea control (Biggins et al. 2010), altering vegetative cover (Milne-Laux and Switzer 2006), reducing shooting pressure on prairie dogs (Pauli and Buskirk 2007), and prairie dog translocation (Truett et al. 2001; Dullum et al. 2005). Adaptive management of prairie dog populations and further investigation of ferret responses to management alternatives are needed to develop methods for increasing the success of ferret reintroduction efforts.

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