EVALUATION AND DEVELOPMENT OF BLACK-FOOTED FERRET RESOURCE SELECTION MODELS

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by

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The undersigned, appointed by the Dean of the Graduate School, have examined the thesis entitled

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CHAPTER TWO

EVALUATION AND DEVELOPMENT OF BLACK-FOOTED FERRET RESOURCE SELECTION MODELS

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ABSTRACT

Resource selection (RSF) and utilization function (RUF) models facilitate habitat evaluations and investigation of theorized mechanisms of space use patterns. We monitored post-breeding (2007-2008) resource selection of adult black-footed ferrets (*Mustela nigripes*) inhabiting the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, South Dakota, USA. Our objectives included (1) evaluation of a recently developed ferret RUF generated from observations of ferrets on an adjacent colony; and (2) development of new RSFs, while evaluating influences on resource selection (e.g., predators and resource connectivity) not yet investigated for *M. nigripes*.

Chapter One: We used the ferret RUF to project the predicted occurrence of ferrets within the South Exclosure, and evaluated model performance via "weighted" compositional analysis and presence count-metrics. Compositional analysis of home range use and colony-level availability, and core area use and home range availability demonstrated ferret selection of the predicted Very High and High occurrence categories. Of all ferret locations, 71.83% (i.e., 329/458) and 72.25% (i.e., 302/418) occurred in areas of Very High or High predicted occurrence in 2007 and 2008, respectively. These results suggested that the RUF was useful in predicting ferret space use; that is, the model could be used to predict ferret occurrence and evaluate fine-scale habitat suitability. Evaluation of RUF performance on Conata Basin colonies of varying resource configuration and size, and black-tailed prairie dog colonies at other sites might increase understanding of the general utility of the RUF.

Chapter Two: We investigated influences of open black-tailed prairie dog burrows, active burrows, edge effects, resource connectivity and predators (coyotes, *Canis latrans*, and American badgers, *Taxidea taxus*) on ferret resource selection. In both years, black-footed ferrets selected areas of increased abundance of active burrows. Such areas might be characterized by increased black-tailed prairie dog density and increased variety of burrow structures. Ferrets selected areas of increased distance from colony edges in 2007; however, a main-effects interaction suggested that if active burrow density was high in an edge area, ferrets still might select the area. Spatial avoidance of coyotes and badgers, or similarities in space use among ferrets and these predators were not evident in our final RSFs. Connectivities of active and open burrow patches also were not retained in our RSFs. Results of this assessment complement previous studies in demonstrating the importance of active burrows in ferret resource selection. Conservation and restoration of colonies of increased active burrow and prairie dog density are needed for continued recovery of ferrets. Our RSFs, if validated via independent data, could complement habitat evaluations by incorporating consideration of fine-scale resource selection into evaluation procedures.

INTRODUCTION

Upon capture of the last-trapped black-footed ferret (*Mustela nigripes*) of the last known extant population of ferrets (February 1987, Meeteetse, Wyoming), recovery of *M. nigripes* "depended on development of an effective captive breeding program" (Lockhart et al. 2006:12). Such a program continues to evolve (Marinari and Kreeger 2006). In 1991 ferrets were available for reintroduction. Evaluation and selection of reintroduction sites became essential components of the ferret recovery program (Biggins et al. 1993, 2006b).

A bioenergetics model (Biggins et al. 1993), derived from previous models (Linder et al. 1972, Hillman et al. 1979, Stromberg et al. 1983, Forrest et al. 1985, Powell et al. 1985, Houston et al. 1986, Miller et al. 1988), has been used to conduct many habitat evaluations. The model provides a means of estimating ferret carrying capacity (i.e., black-footed ferret family rating, BFFR) of a prairie dog (*Cynomys* spp.) complex (i.e., a group of colonies, each ≤ 7 km apart). The model's simplicity affords habitat assessment "with data that are easily and inexpensively collected" (Biggins et al. 1993:74). The performance of this evaluation system has not been rigorously assessed by comparing its predictions with demographic data from corresponding populations of reintroduced ferrets. A cursory look, however, suggests that success (i.e., population growth rates, survival rates, and reproductive output) of ferret populations has been positively correlated with BFFRs (D. E. Biggins, U. S. Geological Survey, personal communication). This reinforces an intuitive notion that success of ferret populations is linked to the coarse-scale abundance and density of prairie dogs in colonies and complexes.

More recently, Biggins et al. (2006b) revised the 1993 model to encourage consideration of territoriality (Biggins et al. 2006a), and to reemphasize consideration of the proportion of complexes occupied by prairie dogs. Also, Biggins et al. (2006a) introduced the concept of the subcomplex (a group of colonies, each ≤ 1.5 km apart).

Estimation of BFFRs allows coarse-scale evaluation of ferret complexes. Consideration of subcomplexes, the proportion of complex occupied by prairie dogs, and the characteristics and reintroduction history of colonies (Livieri 2007) allows evaluation of a prairie dog complex (Biggins eta l. 2006a). As suggested by studies of Meeteetse ferrets, and other populations, resolution might increase further by considering nonrandom space use of ferrets (Biggins et al. 1985, Richardson et al. 1987) and the patchiness of prairie dogs and burrows (e.g., Jachowski et al. 2008) within colonies that allow fine-scale resource selection (Biggins et al. 2006a, Jachowski 2007).

Resource selection function (RSF, Manly et al. 2002) and utilization function (RUF, Marzluff et al. 2004) models aid in incorporating fine-scale densities and distributions of resources into estimating habitat suitability. If available and useful, RSFs or RUFs could be used to project the relative, predicted occurrence of ferrets upon landscapes. Managers could then further prioritize releases of ferrets and conservation/restoration of prairie dog colonies.

The following chapters address fine-scale resource selection of ferrets, under RSF and RUF approaches, and associated implications. Chapter One addresses the ability of a recently developed ferret RUF (Jachowski 2007) to incorporate fine-scale influences of edge-effects and the probabilistic distribution of open active (prey cues, sensu Biggins et al. 1993) burrows in estimating ferret occurrence. The objective was to evaluate accuracy of the RUF in predicting the occurrence of ferrets inhabiting the South Exclosure, a 452-ha black-tailed prairie dog (*C. ludovicianus*) colony in the Conata Basin of southwestern South Dakota, USA. Chapter Two discusses the development of ferret RSFs, and investigation of hypothesized mechanisms of post-breeding space use patterns of ferrets inhabiting the South Exclosure. Within development of RSFs, the chapter evaluates potential influences of all open burrows, active burrows, edge-effects, resource connectivity, and predators/competitors (coyotes, *Canis latrans*, and American badgers, *Taxidea taxus*) on ferret resource selection.

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CHAPTER ONE

EVALUATION OF A BLACK-FOOTED FERRET RESOURCE UTILIZATION FUNCTION MODEL

ABSTRACT

Resource utilization function (RUF) models permit evaluation of potential habitat for endangered species; ideally such models should be evaluated before use. We evaluated the predictive capabilities of a previously developed black-footed ferret (*Mustela nigripes*) RUF. Using the population-level RUF, generated from ferret observations at an adjacent colony, we predicted occurrence of ferrets within a black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, South Dakota, USA. We evaluated model performance, using data collected during post-breeding spotlight surveys (2007-2008), by assessing model agreement via weighted compositional analysis and count-metrics. Compositional analysis of home range use and colony-level availability, and core area use and home range availability demonstrated ferret selection of the predicted Very High and High occurrence categories in 2007 and 2008. Simple year-specific count-metrics also suggested selection of these categories; 71.83% (i.e., 329/458) and 72.25% (i.e., 302/418) of ferret locations occurred in areas of Very High or High predicted occurrence in 2007 and 2008, respectively. Collectively, these results suggested that the RUF was useful in predicting ferret occurrence. Application of the RUF would increase the resolution of habitat evaluations, permitting assessment of habitat suitability within distinct colonies. Additional model evaluation on Conata Basin colonies of varying resource configuration and size, and black-tailed prairie dog colonies at other sites, might increase understanding of influences upon model performance and the general utility of the RUF.

INTRODUCTION

Resource selection by wildlife is of practical significance to wildlife managers (Morrison et al. 1998, Manly et al. 2002). Resource selection functions (RSFs; Manly et al. 2002) often allow for projection of the relative occurrence of a species across a sampled landscape (Manly et al. 2002, Scott et al. 2002, Johnson et al. 2004). Such an approach facilitates conservation of species managed via translocation or reintroduction because managers can assess habitat suitability and prioritize releases before commencing conservation initiatives. Because the applicability of a model might only be specific to the conditions under which the underlying data were collected, however, resource selection models should be evaluated before use, particularly for populations at different sites (Johnson 2001, Shifley et al. 2009).

An assessment of model reliability with independent data provides a robust approach to model evaluation (Power 1992; for examples see Mladenoff et al. 1999, Luck 2002). Such evaluation typically entails comparing values of predicted occurrence to observed values and quantifying the agreement between the two (Shifley et al. 2009), and demonstration that within the current management context, a model is satisfactorily accurate and applicable for its intended purpose (Rykiel 1996). Validation of wildlife models involves consideration of model performance under different conditions (Conroy and Moore 2002), such as another study site or location within the initial study area. Evaluation and validation benefit conservation and management practices by permitting complementary assessments of the strengths and weaknesses, and utility of a model (Starfield and Bleloch 1991, Shifley et al. 2009).

Conservation and management of black-footed ferrets (*Mustela nigripes*) might benefit from a generally robust RSF. Black-footed ferrets are endangered mustelids, highly dependent on prairie dog (*Cynomys* spp.) meat for food (Sheets et al. 1972, Campbell et al. 1987) and burrows for shelter (Forrest et al. 1988, Biggins et al. 2006b). Black-footed ferrets are conserved and managed via captive breeding (Williams et al. 1991, Marinari and Kreeger 2006), and reintroduction (Miller et al. 1994) or translocation (U.S. Fish and Wildlife Service 2006) to increasingly rare habitat (Hoogland 2006, 2007, Slobodchikoff et al. 2009). Evaluations of prairie dog colonies for ferret reintroduction currently involve calculations of the number of ferret families (sensu Biggins et al. 1993) a colony might support, and summation of colony-specific ratings to permit across-complex (i.e., a group of colonies each separated by ≤ 7 km) comparisons (Biggins et al. 1993, 2006c). A robust RSF would aid in evaluating habitat quality within individual colonies by incorporating consideration of fine-scale resource selection in evaluation procedures, perhaps aiding in prioritization of habitat conservation/restoration (Truett et al. 2006, Long et al. 2006, Proctor et al. 2006).

We evaluated a recently developed ferret resource utilization function (RUF) model (Jachowski 2007). Our objective was to determine the model's accuracy in predicting the occurrence of ferrets inhabiting an adjacent, yet distinct, prairie dog colony in the Conata Basin of southwestern South Dakota, USA.

STUDY SITE

The Conata Basin is a 29,000-ha mixed-grass prairie complex (Livieri 2006) important to ferret recovery (Lockhart et al. 2006). We selected a black-tailed prairie dog (*C. ludovicianus*) colony known as the South Exclosure (452 ha) as the site for model evaluation (Fig. 1). The study colony, first inhabited by reintroduced ferrets in 1997 (Livieri 2006), was on lands administered by the U.S. Department of Agriculture (USDA) Forest Service (Buffalo Gap National Grassland), bordered by seasonal water-drainages, and predominantly covered by western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), but with heavily grazed areas dominated by various species of forbs. Active black-tailed prairie dog burrows (sensu Biggins et al. 1993) were irregularly distributed in the colony and physiographic features afforded efficient monitoring of ferrets. Although the study colony is adjacent to the 202-ha, South Dakota colony studied by Jachowski (2007), burrow density (129.3 burrows/ha, vs. 144.7 herein) and distribution, and colony size differed, as did monitored ferrets (see Appendices A and B herein, and Tables 5 and 6 in Jachowski 2007) and adult ferret density (0.0265 and 0.0310 ferrets/ha in 2007 and 2008, respectively; 0.0297 ferrets/ha in Jachowski 2007). Additionally, during our period of study, we found no evidence of inter-colony use of these colonies by adult ferrets.

METHODS

Model Under Evaluation

Jachowski (2007) evaluated resource selection of ferrets using a RUF approach (Marzluff et al. 2004). A RUF, like a RSF (Manly et al. 2002), provides a prediction of species occurrence; however, resources are related to intensity of use in utilization distributions (UDs, Millspaugh et al. 2006). Although Jachowski (2007) evaluated behavioral covariates (proximity of neighbors, space use overlap), we could not project these covariates on the landscape *a priori*. We instead used fitted models that contained the UD of active black-tailed prairie dog burrows (sensu Biggins et al. 1993) and distance to edge of colony, which were the overriding landscape features in the most parsimonious model (Jachowski 2007). Using parameter coefficients from individual, South Dakota animal models ($N = 9$, one randomly selected sample for each of 3 ferrets observed 2005-2006) containing only these covariates, we estimated population-level model coefficients using,

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

where $\hat{\beta}_{ij}$ is the estimate of coefficient i for ferret j (Marzluff et al. 2004, Millspaugh et al. 2006), resulting in the following model:

$$f(x) = 0.0241975479 + 0.0015196232(\mathit{Act\text{-}burrow\text{-}UD}) + 0.0009561196(\mathit{Edge}).$$

The *Act-burrow-UD* parameter represented the UD estimate for the distribution of active black-tailed prairie dog burrows at grid points throughout the evaluation area. The *Edge* parameter represented a raster of Euclidean distances from the 95% volume-contour of the active burrow UD, which represented the colony boundary. We estimated the variance of the population-level model coefficients using

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

which included both intra- and inter-animal variation (*Var*(*intercept*) = 0.0002691695, *Var*(*Act-burrow-UD*) = 0.0000016670, *Var*(*Edge*) = 0.0000080021; Marzluff et al. 2004, Millspaugh et al. 2006).

Prairie Dog Burrow Mapping

Between July and mid-September 2007, we recorded the locations of black-tailed prairie dog burrows on the South Exclosure colony using Trimble® CMT MC-V Global Positioning

System (GPS) receivers (Trimble Navigation Limited, Sunnyvale, CA) mounted on all terrain vehicles (Matchett 1994, Jachowski et al. 2008). We classified burrows, according to access (open vs. plugged) and presence/absence of recent black-tailed prairie dog cues (Biggins et al. 1993), as (1) active (n = 58,633); (2) inactive (n = 6,753); or (3) plugged (n = 2,527). We completed burrow mapping following the first emergence of juvenile black-tailed prairie dogs, but before winter, during the period of greatest black-tailed prairie dog abundance and activity (Hoogland 1995). We limited remapping of burrows by adherence to rows delineated by fluorescent-flags, and by slightly dowsing the edge of mapped burrow openings with DeltaDust®, a deltamethrin formulation used in flea control to halt the spread of plague (Seery et al. 2003, Cully et al. 2006). We downloaded burrow location data using Trimble® GPS Pathfinder® Office 2.1, and differentially corrected locations using U. S. Forest Service, Fort Collins, Colorado, Trimble Community Base Station (http://www.fs.fed.us/database/gps/ftcollins.htm) or Elkhart, Kansas GPS Community Base Station (http://www.fs.fed.us/database/gps/elkhart.htm) correction files in GPS Pathfinder® Office 3.0 (Trimble Navigation Limited, Westminister, Colorado, USA). Correction ranged from 99 to 100% regardless of base station selection, and thus we assume burrow location error ≤ 1 m. We assumed that the distribution of active burrows did not change colony-wide or, changes in this distribution were insufficient to influence the active burrow UD and colony boundary.

Black-footed Ferret Spotlight Surveys

Between 13 June and 10 October 2007, and 11 June and 27 September 2008, we monitored a total of 26 adult black-footed ferrets, including 5 animals that were monitored both years (Appendices A and B), on nearly consecutive nights during spotlight searches (Clark et al. 1984, Campbell et al. 1985, Biggins et al. 2006a) concentrated between midnight and 0600 h (MDT, Biggins et al. 1986, Clark et al. 1986). We established year-specific survey routes that (1) maximized coverage of the survey area, while minimizing overlap, and (2) permitted an evaluation of model performance throughout the entire colony. We trapped and marked adult ferrets in July-August of both years. Intensive surveys (Biggins et al. 2006a) suggested that we monitored all adult ferrets inhabiting the colony.

One observer drove a field vehicle, mounted with a high-intensity 240 BLITZ™ Lightforce™ spotlight (http://www.lightforce.net.au/), 8-16 kmph on a predetermined survey route and, under continuous illumination, maneuvered the spotlight from side to side to detect the emerald green eyeshine of ferrets (Biggins et al. 2006a). We limited disturbance (Campbell et al. 1985) by exposing ferrets to the minimum light required to identify the occupied burrow opening (Biggins et al. 2006a). We identified individual ferrets via unique AVID® Microchip I.D. systems (Folsom, Louisiana) passive integrator transponders (PIT, Fagerstone and Johns 1987, Stoneberg 1996), implanted into ferrets by trained personnel, using automated readers. An automated reader loop antenna encircled the occupied burrow opening and recorded PIT numbers as the ferret emerged (Biggins et al. 2006a). We identified untagged ferrets via unique dye-markings applied to ferrets in early- to mid-June of each field season by trained personnel. We collected Universal Transverse Mercator coordinates of observation locations using hand-held, Garmin® GPS 12XL Personal Navigator® units, rendering accuracy ≤ 15 m.

Because ferrets are capable of traversing entire home ranges in 12 h (Biggins et al. 2006a), we included consecutive locations separated by ≥ 12 h (e.g., Livieri 2007). Nonetheless, 88.13% of consecutive-locations of individual ferrets were separated by ≥ 24h. We estimated home range and core area use of ferrets located ≥ 30 times (Seaman et al. 1999, Millspaugh et al. 2006). Insufficient sample size precluded range and core area estimation of 5 ferrets, including 2 females monitored both years; however, we included these animals in simple count-metric evaluations. We included, and assumed independence of, home ranges and core areas of 1 male and 2 female ferrets monitored both years; these ferrets generally inhabited a different area of the colony (at fine scales) and were neighbored by different ferrets in 2007 and 2008.

Evaluation of Model

We used 2 complementary measures to assess RUF accuracy. We used compositional analysis (use vs. availability, Aebischer et al. 1993) to evaluate whether ferrets selected areas predicted to be of high quality, at two scales of selection (sensu Johnson 1980): home range use vs. colony-wide availability, and core area use vs. home range availability. We also evaluated model accuracy via presence count-metrics; the metrics evaluated model accuracy at used locations only, and thus availability was not considered.

We used the RUF of Jachowski (2007) to develop a map of the predicted occurrence of ferrets in the study colony. Following the methods of Jachowski (2007), we used active burrow locations and a fixed kernel approach (Seaman and Powell 1996, Millspaugh et al. 2006), with bandwidth selected using plug-in methods (Wand and Jones 1995, Jones et al. 1996, Gitzen et al. 2006) and the Kde folder (Beardah and Baxter 1995) in MATLAB® 5.3 (Mathworks Incorporated, Natick, MA) to estimate values of the *Active-burrow-UD* parameter. We used the Euclidean Distance function in ArcGIS® 9.2 to develop a raster of 1-m² cells corresponding to distances to the colony boundary (i.e., 95% volume-contour of the active burrow UD), and then used the raster calculator within ArcGIS®, the Euclidean distance and raw active burrow UD rasters, and the RUF to model the predicted occurrence of black-footed ferrets. We classified predicted occurrence into a four-level, ordered factor based on quantiles (e.g., Rittenhouse et al. 2007), resulting in 4 predicted occurrence classes (Low, Medium, High and Very High; Fig. 1). Quantile classification grouped predicted occurrence grid-cells, each of equal size to *Active-burrow-UD* raster cells, into occurrence categories of equal numbers of features, and thus area.

We developed UD home range estimates for each ferret located ≥ 30 times within one season (Seaman et al. 1999, Millspaugh et al. 2006) using the UD estimation methods described above. We used the 95% volume-contour to delineate the ferret home range boundary. We used the Area Independent Method (AIM; Seaman and Powell 1990, Powell et al. 1997, Powell 2000) to delineate ferret core areas. We first calculated a relative frequency of UD values by dividing point-specific raw UD point-values by the sum of all UD point-values. Next, we calculated the percent of the maximum UD value for each UD point by dividing each value by the highest UD point-value (PCTPROB). We then ranked, from high to low, the UD points by PCTPROB values and defined the percent of the home range represented by each UD value as the percentage of UD points having a value greater than or equal to the UD point under evaluation (PCTRANGE). We plotted PCTRANGE vs. PCTPROB, and defined the core area dividing point as "the point where the plot is maximally distant from a straight line with a slope of -1, the slope of a distribution that cannot be distinguished from random use" (Seaman and Powell 1990:245). We limited estimated core areas to UD points with PCTPROB values (and thus intensity of use values) greater than and equal to the value corresponding to the dividing point.

We overlaid individual ferret UD home range and core area grids on the predicted occurrence map. Because black-footed ferrets rarely extend movements beyond colony boundaries (Biggins et al. 2006b) and are dependent on prairie dog burrows for shelter (Forrest et al. 1988, Biggins et al. 2006b, see also Biggins et al. 1985), we clipped ferret home range and core area estimates (UD grids and polygons) at the colony edge (e.g., Livieri 2007).

We compared home range use versus availability defined at the colony level (second-order selection), and core area use versus availability defined at the home range level (third-order selection, sensu Johnson 1980). We used weighted compositional analysis (Millspaugh et al. 2006), using UDs and core areas to quantify use, because space use of ferrets is often nonrandom (Biggins et al. 1985, Richardson et al. 1986, Jachowski 2007). Within ferret home ranges and core areas, we calculated the UD volume in each predicted occurrence class, summed the UD values by class, and divided the summed UD value by the total UD value of all patches for each class. This approach provided a weighted UD estimate of use for each class of projected occurrence within home ranges and core areas (Millspaugh et al. 2006). Zero-use of a category increases Type I error rates of compositional analysis; we reclassified zero-use as 0.30, the minimum value that reduced such error in a simulation study (Bingham and Brennan 2004, Bingham et al. 2007). We used a statistical significance threshold (α) of 0.10 for tests of selection, and 0.05 for paired *t*-tests.

Using locations of all monitored adult ferrets by year, we calculated presence count-metrics as the number of ferret locations occurring in areas of predicted occurrence (Very High and High; true-positives) and the number of locations occurring in areas of predicted absence (Medium and Low; false-negatives). We categorized apparent off-colony locations as occurring in areas of predicted absence.

A continuum, between absolute inaccuracy and accuracy, might exist in the fit of independent data to model projections. Usefulness is of importance (Box 1979, Shifley et al. 2009). If, in general, ferrets demonstrated selection of areas of Very High or High projected occurrence, we assumed adequate model performance (i.e., usefulness of the model).

RESULTS

Between 13 June and 10 October 2007, and 11 June and 27 September 2008, we collected ≥ 30 observations ($\bar{x} = 39.14$, range = 30-55, $SE = 1.29$) on 11 (8 females, 3 males) and 10 (5 females, 5 males) adult black-footed ferrets, respectively (3 animals monitored both years; Appendices A and B). We used animal locations collected in 2007 (9 females, 3 males, 458 observations, $\bar{x} = 38.17$, range = 12-47, $SE = 2.67$) and 2008 (9 females, 5 males, 418 observations, $\bar{x} = 29.86$, range = 2-55, $SE = 3.88$) in count-metric evaluations (5 ferrets monitored both years, Appendices A and B).

2007.–A comparison between colony-level availability and weighted-use within home ranges demonstrated selection rankings (high to low) of Very High, High, Medium and Low (Wilk's $\lambda = 0.5278$, $\chi^2_3 = 7.0293$, $P = 0.0710$). The Very High class was selected over all other classes, and the High class was selected over the Low and Medium classes (Fig. 2). A comparison between home range availability and core area use demonstrated occurrence rankings of Very High, High, Medium and Low (Wilk's $\lambda = 0.4673$, $\chi^2_3 = 8.3689$, $P = 0.0390$). The Very High and High classes were selected over Medium and Low classes, while the Medium class was selected over the Low class (Fig. 2). Of 458 ferret locations, 71.83% occurred in areas of Very High (n = 211) or High (n = 118) predicted occurrence (Fig. 4).

2008.–A comparison between colony-level availability and weighted-use within home ranges demonstrated selection rankings of High, Very High, Medium and Low (Wilk's $\lambda = 0.4419$, $\chi^2_3 = 8.1671$, $P = 0.0427$). The High class was selected over the Medium and Low classes (Fig. 3). A comparison between home range level availability and core area use demonstrated selection rankings of High, Very High, Medium and Low (Wilk's $\lambda = 0.3664$, $\chi^2_3 = 10.0393$, $P = 0.0182$). The High class was selected over the Low class (Fig. 3). Of 418 ferret locations, 72.25% occurred in areas of Very High (n = 165) or High (n = 137) predicted occurrence (Fig. 4).

DISCUSSION

Compositional analysis and presence count-metrics demonstrated that the Jachowski (2007) RUF adequately predicted locations and intensity of black-footed ferret space use, under our definitions of acceptable performance. Collectively, these results suggest usefulness of the model. Despite potential intersexual differences characteristic of space use by most mustline carnivores (Powell 1979, King and Powell 2007) and inter-ferret variation in duration of colony-residency or level of experience (with the colony, prey, or adult conspecifics), implicating influences of advantages of prior-residency (Biggins et al. 2006b; see also Harwood et al. 2003), the RUF model performed satisfactorily both years, further suggesting utility in predicting ferret space use in black-tailed prairie dog colonies of the Conata Basin.

The RUF could complement evaluations of the suitability of Conata Basin black-tailed prairie dog colonies for ferrets. The current approach for assessing ferret habitat suitability involves coarse-scale evaluations of prairie dog complexes (Biggins et al. 1993, 2006c). This approach is effective in comparing complex suitability; in general, female ferrets inhabiting high rated complexes have reached higher densities and produced larger litters (nearly 2 times larger) than females inhabiting low rated complexes (D. E. Biggins, U. S. Geological Survey, personal communication). However, recent studies implicate consideration of fine-scale colony attributes when evaluating ferret habitat. Black-footed ferrets appear to select areas of high open burrow (Biggins et al. 2006b) and active burrow density (Jachowski 2007, Chapter Two), likely because burrows afford refuge from some predators (Biggins 2000) and inclement weather (Miller et al. 1996), and active burrow densities might correlate with densities of prairie dog prey (Biggins et al. 1993, 2006c, 2006d, Johnson and Collinge 2004; but see Powell et al. 1994, Severson and Plumb 1998). Recent analyses also implicate fitness advantages of areas of relatively high burrow density (D. E. Biggins, personal communication). Accordingly, fine-scale measures of resource distributions within colonies, such as those incorporated in the Jachowski (2007) RUF, would facilitate evaluation of habitat suitability within colonies of a complex.

The Biggins et al. (1993, 2006c) method facilitates evaluation of entire complexes, while the Jachowski (2007) RUF permits prediction of the occurrence of ferrets within distinct colonies and encourages assessment of the probabilistic (UD) distribution of active burrows throughout colonies. Collectively, the two approaches provide a coarse- and fine-scale assessment of ferret habitat suitability. The ferret RUF (Jachowski 2007) could serve multiple purposes. Managers can compare suitability of release locations within distinct colonies, perhaps increasing release site fidelity, reproductive success and survival. Demographic data are needed to more fully evaluate the RUF (Van Horne 1983, Johnson 2007, Shifley et al. 2009); behavioral data (e.g., space use) provide a first approximation of model performance, while data on survival and reproduction provide insight into the utility of a model in predicting population viability consequences. Across-colony comparisons of habitat suitability could be completed under consideration of the "structure" of the occurrence map, such as the number of peaks above various predicted occurrence values, distances between peaks, and perhaps area of peaks.

A resource selection model, or models, if easily applicable, could serve as the central component(s) of habitat evaluations for ferrets. However, although the Jachowski (2007) RUF performed adequately at our study site, it might be difficult to utilize when evaluating expansive areas. Model implementation requires sufficient quantitative performance, as was demonstrated for the South Exclosure colony, but also an appropriate application environment (Shifley et al. 2009). The RUF, at present, requires ground-based mapping and categorization of burrow activity in a colony, an expensive and labor intensive task. Dynamics of burrow activity over 6 and 11 year periods suggested periodic spatial oscillations (Jachowski et al. 2008) that might ultimately influence estimates of ferret occurrence, and perhaps habitat quality. Accordingly, when utilizing the Jachowski (2007) RUF, if continuing to release ferrets to a colony, burrows should be periodically mapped to continually monitor fine-scale suitability; additional research is needed to determine an appropriate inter-mapping interval, which might vary by site. Such difficulties could currently preclude use of the RUF in some contexts. Nonetheless, our evaluation suggests utility of resource selection models in evaluating ferret habitat, indicating the need for (1) a RUF or RSF model that does not require ground mapping, or (2) a method to quickly and cheaply map burrows and classify activity. Remote sensing might afford such an approach; for instance, satellite imagery aided in mapping great gerbil (*Rhombomys opimus*) burrows in Kazakhstan (Davis et al. 2008).

Wildlife resource selection models, like all models, are inherently "wrong"; however, as discussed by Box (1979), "some models are useful". Validation, particularly via independent data (Power 1992), reduces uncertainty and demonstrates model utility under certain contexts. Our evaluation suggested the ferret RUF was useful in predicting ferret occurrence in a black-tailed prairie dog colony of the Conata Basin, and could be utilized when burrow mapping is completed. Others have also used independent data to validate models of wildlife-habitat relationships (e.g., Mladenoff et al. 1999, Roloff et al. 2001, Luck 2002, Mitchell et al. 2002). Often, however, RSF or RUF models are applied without such validation. Increasing reliance on models in wildlife management (Millspaugh and Thompson 2009) underscores the importance of validation. It is possible that selected models do not explain a sufficient amount of variation to be useful. Identifying the conditions under which models are useful is a prerequisite to model application (Shifley et al. 2009). When completed using independent data, model evaluation can help determine the conditions under which a model is appropriate (i.e., a model can be validated). When site-specific models are available, such validation can help evaluate the importance of different variables across a species range and the utility of different models.

MANAGEMENT IMPLICATIONS

The Jachowski (2007) RUF was useful in predicting the occurrence of ferrets on our study colony. Managers could use the model, in conjunction or independent of coarse-scale evaluation (Biggins et al. 1993, 2006c), to evaluate fine-scale suitability of Conata Basin black-tailed prairie dog colonies for ferrets. Burrow mapping is currently a prerequisite to utilization of the RUF. As with all models, predictions of the Jachowski (2007) ferret RUF might be unsatisfactory if context varies sufficiently. At the Conata Basin in 2008, sylvatic plague (caused by the bacterium *Yersinia pestis*), which decimated black-tailed prairie dogs in areas of the complex other than the South Exclosure, could impact reliability of the RUF. Given heterogeneity of burrows within colonies, and the diversity of shapes and sizes of black-tailed prairie dog colonies, the RUF should be reevaluated on colonies of different size/shape and resource configuration within and outside the Conata Basin. In some instances, behavioral mechanisms (e.g., territoriality) might also influence RUF performance; ideally the RUF should be evaluated using demographic data (Van Horne 1983, Johnson 2007, Shifley et al. 2009). Such research would aid in identifying strengths and weaknesses of the RUF. Given the apparent usefulness of the RUF, in general, we encourage development of resource selection models for ferrets on white-tailed (*C. leucurus*) and Gunnison's prairie dog (*C. gunnisoni*) habitat.

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Figure 1. Predicted occurrence (four-level, ordered factor) of black-footed ferrets (*Mustela nigripes*) on the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin (inset map), Buffalo Gap National Grasslands, South Dakota, USA. Projected ferret occurrence was derived from a resource utilization function model (Jachowski 2007) estimating effects of active prairie dog burrow distribution (*Act-burrow-UD*) and colony-edge (*Edge*) on ferret space use. The South Exclosure is immediately southwest of the South Dakota colony utilized by Jachowski (2007).

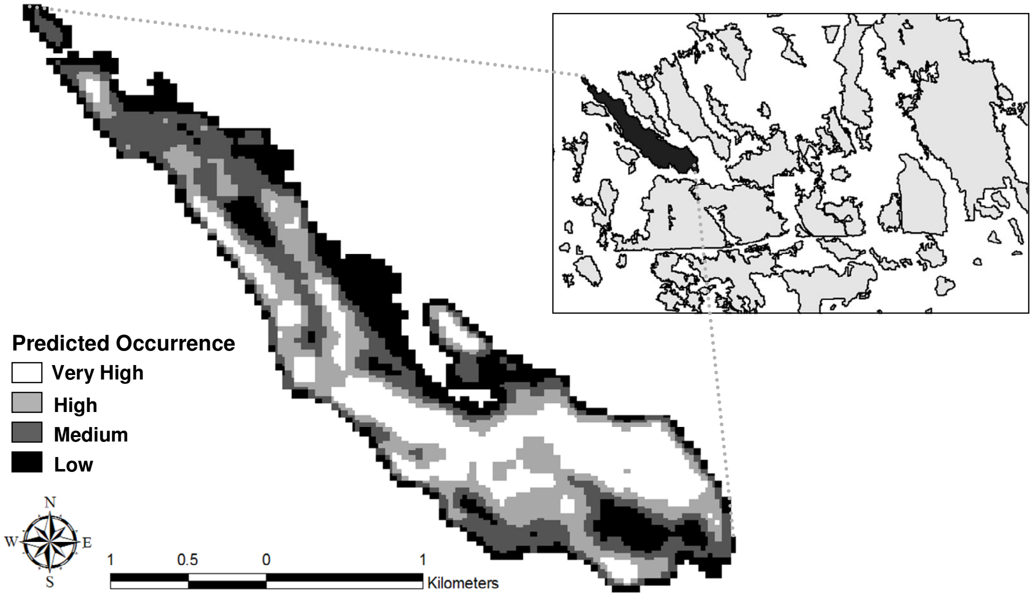


Figure 2. Proportional use and availability (± 1 *SE*), of 4 classes of predicted occurrence, for 11 black-footed ferrets (*Mustela nigripes*) monitored (≥ 30 locations) between 13 June and 10 October 2007 on the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, Buffalo Gap National Grasslands, South Dakota, USA. Graphs correspond to (A) weighted (utilization distribution [UD] volume) use of classes of predicted occurrence in 95% volume-contour UD home ranges compared to colony-level availability of the classes and (B) weighted use of classes in Area Independent Method core areas compared to home range availability (unweighted) of the classes. Classes sharing underscore were not significantly different (α = 0.05) based on paired *t*-tests.

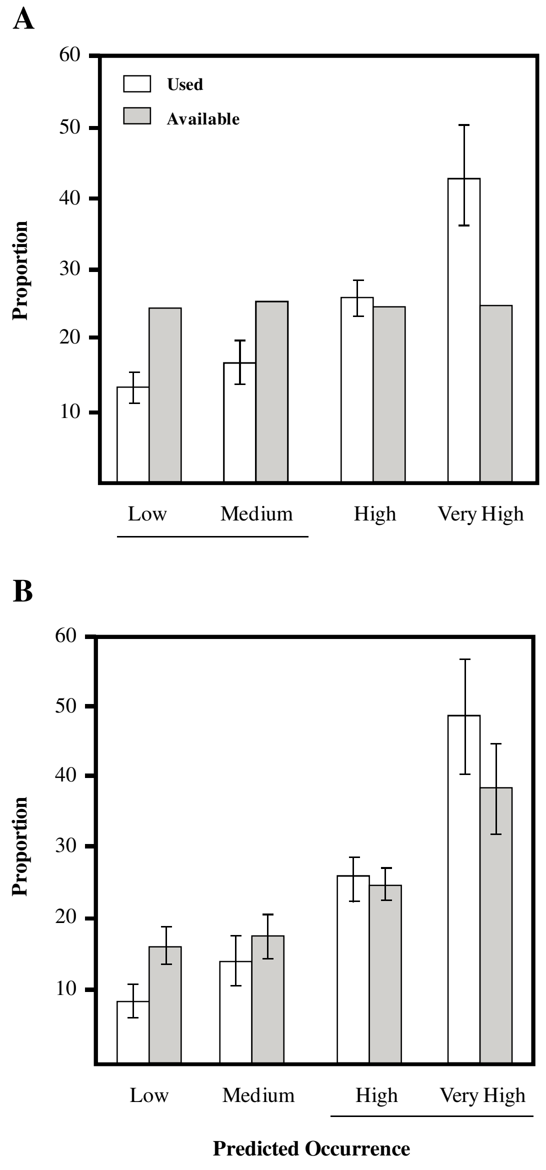


Figure 3. Proportional use and availability (± 1 *SE*), of 4 classes of predicted occurrence, for 10 adult black-footed ferrets (*Mustela nigripes*) monitored (≥ 30 locations) between 11 June and 27 September 2008 on the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, Buffalo Gap National Grasslands, South Dakota, USA. Graphs correspond to (A) weighted (utilization distribution [UD] volume) use of classes of predicted occurrence in 95% volume-contour UD home ranges compared to colony-level availability of the classes and (B) weighted use of classes in Area Independent Method core areas compared to home range availability (unweighted) of the classes. Classes sharing underscore were not significantly different (α = 0.05) based on paired *t*-tests.

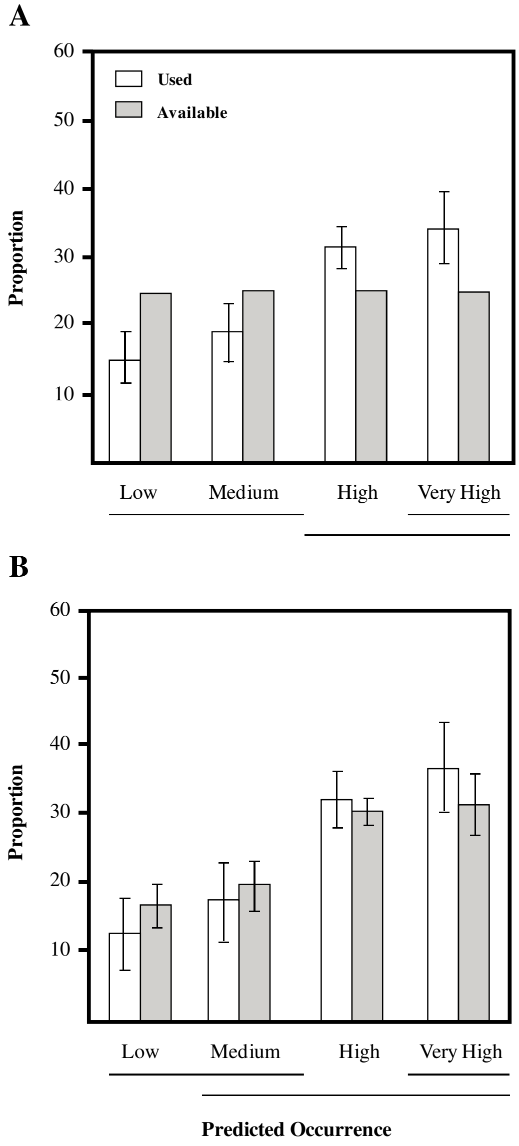
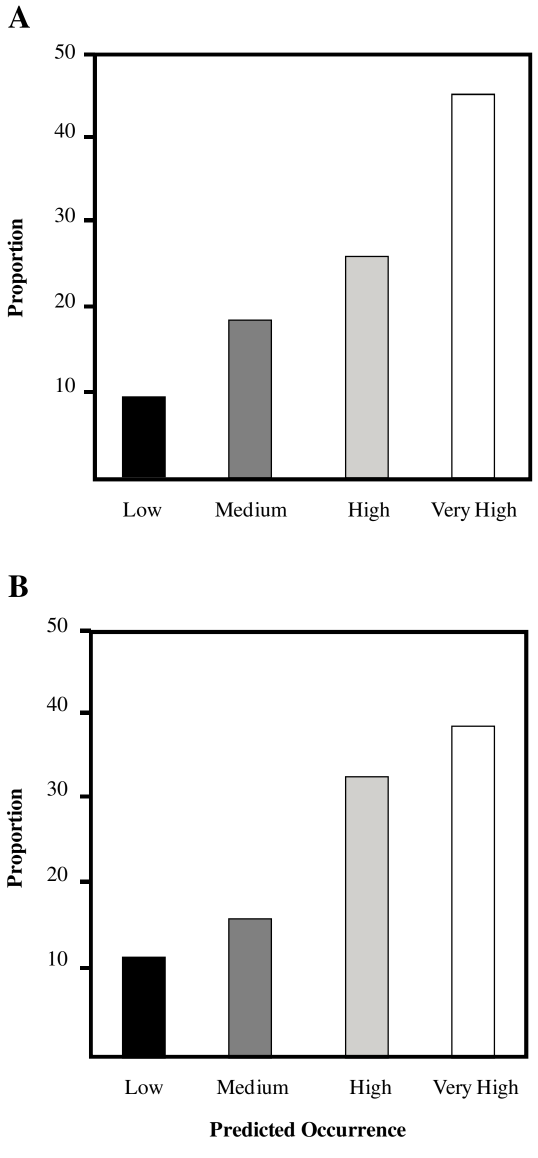


Figure 4. Proportion of black-footed ferret (*Mustela nigripes*) observation locations (collected via spotlight surveys) in each class of predicted occurrence (see Fig. 1) between (A) 13 June and 10 October 2007 (*n* = 12 ferrets, 457 observations included) and (B) 11 June and 27 September 2008 (*n* = 14 ferrets, 413 observations included) on the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, Buffalo Gap National Grasslands, South Dakota, USA.



CHAPTER TWO

POST-BREEDING RESOURCE SELECTION OF BLACK-FOOTED FERRETS IN THE CONATA BASIN, SOUTH DAKOTA

ABSTRACT

Resource selection function (RSF) models aid in evaluating habitat suitability and investigating hypothesized mechanisms of space use of wildlife. We investigated post-breeding resource selection of endangered black-footed ferrets (*Mustela nigripes*) on a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin of South Dakota, USA, during 2007-2008 under a RSF approach. We evaluated influences of all open burrows, open active burrows characterized by prairie dog cues, edge-effects, resource connectivity and predators/competitors (coyotes, *Canis latrans*, and American badgers, *Taxidea taxus*). In both years, black-footed ferrets selected areas of increased abundance of active burrows; such areas were characterized by increased refuge and, perhaps, prairie dog density. Ferrets selected areas at increased distances from colony edges in 2007; however, an interaction suggested ferrets selected areas near an edge if active burrow density was high. Spatial avoidance of coyotes and badgers, or similarities in space use among ferrets and these predators were not evident in our final RSFs. Connectivities of all open and active open burrow patches also were not retained in our RSFs. Our results complement previous studies that demonstrated the importance of active burrows in ferret resource selection. Conservation and restoration of colonies of increased burrow and prairie dog density are needed for continued recovery of *M. nigripes*. Our RSFs, if validated, could complement coarse-scale habitat evaluations by providing fine-scale assessments of habitat suitability.

INTRODUCTION

Resource selection involves behavioral responses of wildlife to environmental and physiological stimuli (Hilden 1965), resulting in disproportionate use of some resources relative to others (Johnson 1980). Generally it is assumed that animals select resources in a manner that most efficiently satisfies life history requirements, and thus increases fitness (Pulliam and Danielson 1991, Martin 1998). Such fitness consequences suggest important implications of resource selection (Morrison et al. 1998), particularly in conservation programs such as that of the endangered black-footed ferret (*Mustela nigripes*), an obligate predator of prairie dogs (*Cynomys* spp.; Sheets et al. 1972, Campbell et al. 1987) and inhabitant of prairie dog colonies (Forrest et al. 1988, Biggins et al. 2006c).

Currently ferrets are conserved via captive propagation (Williams et al. 1991, Marinari and Kreeger 2006) and reintroductions (Miller et al. 1994a) to pre-evaluated prairie dog complexes (i.e., prairie dog colonies ≤ 7 km apart, Biggins et al. 1993, 2006d). Advances in recovery continue (Lockhart et al. 2006); however current numbers suggest reintroduction has "succeeded" (sensu U. S. Fish and Wildlife Service [USFWS] 2006) at few sites. Although numerous factors might mediate recovery success (Miller et al. 1996, Reading et al. 1996, Biggins and Godbey 2003), 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, see also Luce 2006). All species of *Cynomys* are of conservation concern (Hoogland 2006, 2007, Slobodchikoff et al. 2009). Since the early 1900's, 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 (Barnes 1993) and ferrets (Godbey et al. 2006) are highly susceptible. Declining prairie dog numbers have increased the relevance of identifying complexes suitable for ferret reintroduction. Once identified, complex (Biggins et al. 1993) and, more recently, subcomplex (i.e., prairie dog colonies ≤ 1.5 km apart, Biggins et al. 2006d) suitability are evaluated. Given heterogeneity of burrows (Biggins et al. 2006c, Jachowski et al. 2008) and prairie dogs (Hoogland 1995) within distinct colonies, and nonrandom space use of ferrets (Biggins et al. 1985, Richardson et al. 1986, Jachowski 2007), evaluation of fine-scale resource distributions and habitat suitability are also needed.

Resource selection function (RSF) models (Manly et al. 2002) might aid in evaluating fine-scale habitat suitability, conserving prairie dog colonies, and prioritizing ferret reintroductions. The utility of RSFs lie in their ability to incorporate important fine-scale resources into estimating habitat suitability (Manly et al. 2002). Species occurrence can then be predicted and projected upon landscapes (Manly et al. 2002, Scott et al. 2002, Johnson et al. 2004). Although numerous factors might mediate habitat suitability for ferrets, previous research on ferrets and other mustelids implicates particular importance of certain resource attributes. Densities and distributions of refuge and prey influence space use of many mustelids (Erlinge and Sandell 1986, Fagerstone 1987, King and Powell 2007), including ferrets (Biggins et al. 2006c); however, a surrogate measure of prairie dog density was used (Jachowski 2007). Resource or habitat connectivity (Taylor et al. 1993, With et al. 1997, Crooks and Sanjayan 2006) 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 mustelids (Gehring and Swihart 2004). Colony edges influenced resource selection of ferrets, albeit variably, on a South Dakota black-tailed prairie dog (*C. ludovicianus*) colony (Jachowski 2007); however, reasons for such variation were not evaluated. Influences of resource connectivity have not yet been addressed for ferrets.

Development of RSFs might also allow investigation of influences of competitors/predators on space use. Intraguild predation and competition might influence resource selection (Polis et al. 1989, Palomares and Caro 1999, Linnell and Strand 2000, Creel et al. 2001, Donadio and Buskirk 2006), often of the smaller species (Hunter and Caro 2008). Predation by coyotes (*Canis latrans*) and American badgers (*Taxidea taxus*) on established (Forrest et al. 1988) and reintroduced (Biggins 2000, Biggins et al. 1998, 2006a) ferrets, and selection of prairie dog prey by badgers inhabiting prairie dog colonies (Goodrich and Buskirk 1998), implicate potential influences of these particular carnivores. Direct influences of coyotes and badgers on ferret survival are evident (e.g., Biggins et al. 2006a); however, influences of these predators on ferret space use are unclear.

We investigated post-breeding resource selection by adult black-footed ferrets inhabiting a black-tailed prairie dog colony in South Dakota, USA, during 2007-2008. We aimed, mainly, to develop robust predictive RSFs of ferret occurrence on black-tailed prairie dog colonies. We also aimed to evaluate potential influences of coyotes and badgers, resource connectivity, and density of all open burrows and active open burrows on resource selection of ferrets.

STUDY SITE

We conducted our study on a 452-ha black-tailed prairie dog colony known as the South Exclosure (Fig. 1), a colony of the 29,000-ha Conata Basin in southwestern South Dakota (Livieri 2006). The colony, which was inhabited by ferrets of captive-ancestry since reintroductions in 1997 (Livieri 2006), was on land administered by the U.S. Department of Agriculture (USDA) Forest Service (Buffalo Gap National Grassland). The northern tip of the colony extended into Badlands National Park. The site was bordered by seasonal water-drainages and badland buttes, and predominantly covered, heterogeneously, by western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), and buffalo grass (*Buchloe dactyloides*), along with mixed forbs in heavily grazed areas. Prairie dog density was estimated (Biggins et al. 1993) at 41.03 black-tailed prairie dogs/ha. Average monthly temperature and precipitation were 21.89 °C and 4.28 cm in 2007 (June-October), and 21.94 °C and 7.86 cm in 2008 (June-September), respectively (South Dakota Office of Climatology, http://climate.sdstate.edu/climate_site/climate.htm).

METHODS

Prairie Dog Burrow and Colony Mapping

Between July and mid-September 2007, the period of greatest black-tailed prairie dog abundance and activity (Hoogland 1995), we recorded the locations of black-tailed prairie dog burrows using Trimble® CMT MC-V Global Positioning System (GPS) receivers (Trimble Navigation Limited, Sunnyvale, CA) mounted on all terrain vehicles (Matchett 1994, Jachowski et al. 2008). We classified burrows as (1) active (prairie dog cues, *n* = 58,633); (2) inactive (absence of prairie dog cues, *n* = 6,753); or (3) plugged (*n* = 2,527) under the methods of Biggins et al. (1993). To limit remapping, we adhered to rows delineated by fluorescent-flags and dowsed the edge of mapped burrow entrances with DeltaDust®, a deltamethrin used in flea control to halt the spread of plague (Seery et al. 2003, Cully et al. 2006). We downloaded burrow location data using Trimble® GPS Pathfinder® Office 2.1, and differentially corrected locations using U. S. Forest Service, Fort Collins, Colorado, Trimble Community Base Station (http://www.fs.fed.us/database/gps/ftcollins.htm) or Elkhart, Kansas GPS Community Base Station (http://www.fs.fed.us/database/gps/elkhart.htm) correction files in GPS Pathfinder Office® 3.0 (Trimble Navigation Limited, Westminister, Colorado, USA). Correction ranged from 99 to 100%. We assume location error ≤ 1 m, and that burrow activity did not change between 2007 and 2008.

Prairie dog colony boundaries are delineated in many ways (Biggins et al. 2006e). Ferrets often limit their non-dispersal movements to areas with prairie dog burrows (e.g., Biggins et al. 1985, 2006c). At fine scales, ferrets might perceive an area in which burrows are nonexistent to be a habitat edge. We buffered all open burrows, in ArcGIS® 9.2 (Environmental Systems Research Institute, Redlands, California, USA), by 20-m circular polygons. We “dissolved” overlapping polygons to create a colony boundary. The colony thus included a buffer of 20 m beyond the outermost burrows and excluded interior areas >20 m from the nearest burrow opening. We assume this boundary was constant between 2007 and 2008.

Spotlight Surveys

We monitored black-footed ferrets (Appendices A and B), American badgers and coyotes during spotlight surveys (Clark et al. 1984, Campbell et al. 1985, Biggins et al. 2006b). We estimated ferret population size via trapping in July-August, of both years, during one or more 3-4 night periods (Biggins et al. 2006b). Estimates suggested that we monitored all adult ferrets, each year. We monitored 5 ferrets both years. Area of occupancy (at fine scales) and identity of neighboring ferrets varied from to 2007 to 2008 for each of these ferrets; therefore we assumed inter-year independence of resource selection. We did not estimate numbers of badgers or coyotes inhabiting or traversing the colony.

We conducted surveys, concentrated between midnight and 0600 h (MDT, Biggins et al. 1986, Clark et al. 1986), on nearly consecutive nights. 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 kmph and, under continuous illumination, maneuvered the spotlight to detect the eyeshine of each carnivore species (Biggins et al. 2006b). We limited disturbance (Campbell et al. 1985) by exposing animals to the minimum light required to identify the occupied burrow opening or location. Age and individual identification was not discernable for coyotes or badgers. We identified "tagged" ferrets via unique AVID® Microchip I.D. systems (Folsom, Louisiana) passive integrator transponder (PIT) identification numbers accumulated using automated readers (Fagerstone and Johns 1987, Stoneberg 1996, Biggins et al. 2006b); as a ferret passed near the reader loop antenna, which surrounded the occupied burrow entrance, the unit recorded PIT numbers of the ferret (Biggins et al. 2006b). We identified "untagged" ferrets via unique dye-markings established by trained personnel in early- to mid-June of each field season. All trapping and marking of ferrets met guidelines of the American Society of Mammalogists (Gannon et al. 2007).

We collected Universal Transverse Mercator coordinates of observation locations using hand-held, Garmin® GPS 12XL Personal Navigator® units (≤ 15 m accuracy). We included consecutive, confirmed locations of individual ferrets separated by ≥ 12 h in analyses (e.g., Livieri 2007); 88% of consecutive-locations of individual ferrets were separated by ≥ 24h. We included all confirmed observations of coyotes and badgers. We collected one location if we observed two or more coyotes or badgers together (Hurlburt 1984). On a few occasions, we observed a coyote near a badger that was excavating a burrow (Minta et al. 1992); we collected one location for each species. We observed swift foxes (*Vulpes velox*), another potential mammalian predator of ferrets, on 3 confirmed occasions.

Data Analyses

We developed RSFs by relating intensity of ferret use (population level) to resource attributes within a colony-wide system of grid cells. We aimed to limit spatial autocorrelation of resources among neighboring cells to increase the likelihood that selection of resources in one cell would be independent from selection of resources in neighboring cells. Additionally, reduction of autocorrelation increases precision of estimated standard errors, and reduces the likelihood of Type I error (Hurlburt 1984).

We used open and active burrows to evaluate spatial autocorrelation. We used Hawth's Tools (Beyer 2004) to establish vector grid-systems of various square cell sizes (between 40 m and 130 m, at 5 m intervals), each encompassing the extent of the black-tailed prairie dog burrow map. We counted the number of open and active burrows in each grid cell, of each grid-system. We limited grid cells to those containing ≥ 1 open or active burrow. We evaluated spatial autocorrelation of each resource using Moran's I (Moran 1950, Cliff and Ord 1981). We conceptualized the spatial relationship of cells as all neighboring cells ($n = 8$) and interpreted Moran's I as a global measure of spatial autocorrelation of each grid system. We plotted Moran's I values against grid cell sizes and interpreted distances at which Moran's I leveled off (i.e., no longer increased or decreased) as grid-systems in which spatial autocorrelation was minimized. Spatial autocorrelation of both burrow types declined with increasing grid cell size, leveled off at 80 m, then declined at distances > 90 m until leveling off again at ~110 m (Fig. 2). For our investigation of fine-scale resource selection, we used the 80 m by 80 m grid system. Autocorrelation was not eliminated, but was limited at our preferred scale of assessment.

We related cell-specific intensity of ferret use to cell-specific attributes. We counted the number of ferret locations (response variable), and the number of open burrows, active burrows, and coyote and badger locations (predictor variables) per cell (Table 1). We then calculated the Euclidean distance from the center of each cell to the nearest colony edge (Table 1). We also assigned each cell contiguity (connectivity) scores for open burrows and active burrows (Table 1). We categorized cells according to a 5-level, ordered factor based on quantiles of open and active burrow counts. Quantile classification grouped grid-cells into categories of equal numbers of cells. This delineated "patches" of cells of similar quantile values; these values did not serve as resource attributes, however. We calculated a contiguity index for each cell (FRAGSTATS, McGarigal et al. 2002) using,

$$\frac{\left[\frac{\sum_{r=1}^{Z} c_r}{a}\right]-1}{v-1},$$

where c is the contiguity value for cell r, a is the area of cell r (0.64 ha), and v is the sum of quantile values in the focal and neighboring (n = 8) cells. We weighted cell-specific contiguity values by corresponding open or active burrow counts; increasing scores indicated increasing cell-connectivity and density of open or active burrows.

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 first evaluated all single parameter models, retaining the variable with the lowest AIC_c value (Burnham and Anderson 2002), and then evaluated two parameter models, retaining the model of lowest AIC_c value. We continued this process until a deviance ratio test (DRT, 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). For the 2007 model, which contained 2 variables, we checked for a main-effects interaction, and assessed model significance, relative to the main effects model, using a DRT. We retained the significant interaction and associated main effects in the final model (McCullagh and Nelder 1989). We assessed statistical significance of the final RSFs, relative to a null model (intercept-only), using DRTs. 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. With a model training-to-testing ratio of 80:20, we divided grid cell data into 5 random subsets. We iteratively withheld one subset, fit the regression model using the 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 scores. When consecutive bins contained no observations, we simplified the 32 bins accordingly. Using a Spearman-rank correlation, 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

Between 13 June and 10 October 2007 (*n* = 12 ferrets), and 11 June and 27 September 2008 (*n* = 14 ferrets), we collected 458 ($\bar{x}$ = 38.17, *SE* = 2.67, range = 12 - 47) and 418 ($\bar{x}$ = 29.86, *SE* = 3.88, range = 2 - 55) observations of adult ferrets, respectively. We collected 106 and 163 badger locations, and 66 and 35 coyote locations in 2007 and 2008, respectively. Average open burrow and active open burrow grid cell counts were 83.93 (*SE* = 1.76; range = 1 - 216) and 75.27 (*SE* = 1.62, range = 0 - 190), respectively. Average distance of cell centers to the nearest colony edge was 130.72 m (*SE* = 3.98, range = 0 - 479.13).

The 2007 RSF suggested that adult black-footed ferrets selected areas with increased active burrow density and distance to colony edge (Table 2); no other parameter was included in the final model. An interaction (Active burrow × Edge) demonstrated ferrets selected areas of increased active burrow abundance near colony edges, suggesting edge-effects might be conditional upon active burrow abundance (Fig. 3). A DRT indicated good model fit (DRT = 6.41, *df* = 3, *P* = 0.0933) and cross-validation indicated good model performance for all *k*-fold sets (Table 3).

The 2008 RSF suggested that adult black-footed ferrets selected areas with increased active burrow density (Table 2); no other variable was retained in the final model. A DRT indicated good model fit (DRT = 4.27, *df* = 1, *P* = 0.0389) and cross-validation indicated good model performance for all *k*-fold sets (Table 3).

DISCUSSION

In both years, black-footed ferrets selected areas with increased active burrow abundance, which corroborates other findings from the Conata Basin that suggested ferrets concentrate space use in areas of increased active burrow density (Jachowski 2007, Livieri 2007). Active burrow density often positively correlates with prairie dog density (Biggins et al. 1993, 2006d, 2006e, Johnson and Collinge 2004; but see Powell et al. 1994, Severson and Plumb 1998) suggesting ferrets selected areas of increased prairie dog abundance. Various theoretical and empirical studies indicate that predators should select areas of increased prey abundance (review in Sih 2005), termed the aggregative response (Hassell 1978). Such selection has been suggested for various *Mustela* species (*M. erminea* [Erlinge and Sandell 1986, Murphy and Dowding 1995, Hellstedt and Henttonen 2006]; *M. frenata* [Gehring and Swihart 2003, 2004]; *M. furo* [Norbury et al. 1998]; *M. nivalis* [Klemola et al. 1999, Sönnichsen and Szafrańska 2008]; *M. putorius* [Danilov and Rusakov 1969]). Prairie dogs typically comprise ≥ 90% of the ferret's diet (Sheets et al. 1972, Campbell et al. 1987), indicating ferrets, particularly maternal females (Powell 1979, Sandell 1989), should select areas of increased prairie dog density. However, active burrow density is a surrogate measure of prairie dog density (Biggins et al. 1993, 2006d, 2006e, Johnson and Collinge 2004). An assessment of spatial relationships between ferrets and actual prairie dogs is needed. Because prairie dogs might avoid areas occupied by ferrets (Hillman and Linder 1973, see also Martin et al. 1984), dynamic interactions might require consideration, particularly when investigating selection at very fine scales (e.g., within prairie dog social units, termed coteries; King 1955).

As emphasized by Biggins et al. (1993, 2006c), when active burrow density correlates with prairie dog density, areas of high active burrow density provide ferrets not only with high densities of prairie dogs, but immediacy of refuge from some predators. Similar cases exist for short-tailed (King and Powell 2007:183) and long-tailed weasels (Gehring and Swihart 2003) which use fencerows or stone walls that provide antipredator cover and increased density of small mammalian prey, and more generally, species that hunt within and use refuge used by prey. The lack of retention of the all open burrow variable in RSFs does not indicate unimportance of refuge; 86% of black-tailed prairie dog burrows were active on our study colony. On the study colony, areas of high active burrow density were also areas of high refuge density.

Areas of high burrow density might also be characterized by a greater variety of burrow types. Excavations of prairie dog burrows indicate structural heterogeneity (review in Verdolin et al. 2008) that might permit selection. Black-footed ferrets, like other mustelids (King and Powell 2007), are killed by semifossorial predators (namely badgers) and are sensitive to thermal stress (Harrington et al. 2006). Ferrets might select dens for their complexity (Forrest et al. 1985, Sheets et al. 1971), depth or temperature (Harrington et al. 2006), scales of selection not considered in our analyses. Data collected on ferrets inhabiting white-tailed prairie dog (*C. leucurus*) colonies of a Wyoming complex suggest ferrets select burrow systems with multiple openings to the surface (D. E. Biggins, U. S. Geological Survey, unpublished data). Siberian polecats (*M. eversmanni*, Stroganov 1969), a close relative of the black-footed ferret (O'Brien et al. 1989), and short-tailed weasels (King and Powell 2007:217) also appear to select for characteristics of den sites.

Colony edges appeared to influence resource selection of ferrets in 2007, but not in 2008. Previous research, albeit under methods of evaluation and colony edge classification not used herein, suggested an edge-effect might be positive or negative; some ferrets apparently avoided colony edges, while some ferrets appeared to select areas near colony edges (Jachowski 2007). The 2007 edge-effect herein was dependent upon active burrow abundance; if active burrow density was high near a colony edge area, ferrets selected the area. Ferrets might inhabit areas near colony edges of low or high active burrow density. Variability in area of occupancy by ferrets within a colony might explain variable edge-effects reported by Jachowski (2007), and the interaction between the active burrow and edge variables in the 2007, but not in the 2008 RSF.

Edge-associated costs, if they exist, are currently unclear for ferrets. Given sufficient refuge density in an edge area, potential benefits might be numerous. For instance, ferrets might use edge areas, of high burrow abundance, as corridors to traverse prairie dog colonies. Also, like other predators (see Sih 2005), ferrets might concentrate space use in areas of increased plant abundance where herbivore productivity and abundance might be greatest. Vegetation at colony edges is often characterized by short- (e.g., *Bouteloua gracilis* and *Buchloe dactyloides*) and mixed-grasses (e.g., *Pascopyrum smithii*; Koford 1958, Garrett et al. 1982, Cincotta 1985, Cincotta et al. 1989), species frequently consumed by black-tailed prairie dogs in many studies

(Tileston and Lechleitner 1966, Summers and Linder 1978, Fagerstone et al. 1981, Garrett et al. 1982, Uresk 1984, Lehmer et al. 2006). Prairie dogs inhabiting such areas might produce more offspring; in one study, female black-tailed prairie dogs produced more pups in areas (albeit not edge) comprised mainly of grasses, relative to areas characterized by forbs (Cincotta 1985). Our general impression, particularly in 2007, was that abundance of grasses and black-tailed prairie dogs (visual counts, Fagerstone and Biggins 1986), particularly juveniles, were greatest near certain colony edges. A recent study indicates that ferrets might selectively prey upon juvenile black-tailed prairie dogs (D. E. Biggins, personal communication), further suggesting rewards to areas comprised of grasses.

General influences of predators on the behavioral decisions of prey (Lima and Dill 1990, Caro 2005), and frequent predation on ferrets (e.g., Forrest et al. 1988) suggest potential effects of predators on ferret resource selection. Coyotes and badgers might not only kill, but also compete with ferrets for prey, and thus influence ferret space use. However, neither coyote nor badger influences were supported in RSF models. We do not interpret this outcome as indicating lack of influences of these carnivores, or predators in general. In light of increasing evidence of carnivore-influences on the behavior of other carnivore species (review in Linnell and Strand 2000), including mustelids (Sidorovich and Macdonald 2001, Aunapuu and Oksanen 2003, Harrington and Macdonald 2008), alternative explanations should be considered. Black-footed ferrets might behaviorally reduce costs of proximity to predators/competitors without absolute spatial avoidance. Ferrets can often escape coyotes by submerging in burrows, rather than shifting activity areas. If burrow density is sufficient, spatial avoidance of coyotes might not be required; ferrets might instead avoid time periods of increased coyote activity (Biggins 2000). When conditions, such as nighttime activity of rabbits, favor increased use of prairie dog colonies by coyotes at night, however, predation risk might increase for ferrets (Biggins 2000).

Spatial avoidance of areas used by *T. taxus* might be difficult. Badgers might select prairie dog prey (Goodrich and Buskirk 1998), and thus might select areas of increased prairie dog density. Also, in one study badgers excavated 17 of 18 burrows baited with prairie dog meat (Biggins et al. 1991), suggesting attraction to prairie dog carcasses, such as those in ferret dens (Richardson et al. 1987; see Creel et al. 2001:48). Although badgers excavate burrow systems

(Lindzey 2003, Michener 2004), selection of den sites with multiple escape holes, as suggested above, or use of multiple dens by ferrets, as exhibited by kit foxes (*Vulpes macrotis*) in areas inhabited by coyotes (White et al. 1994), might aid in defense. In one study, ferrets cached prey in multiple burrow systems (Richardson et al. 1987), suggesting use of multiple dens, perhaps even within short timeframes. If selecting dens with multiple openings, and caching prey in multiple den sites, ferrets might be able to avoid badgers and reduce costs associated with loss of prey. Although this suggests spatial avoidance, such avoidance might occur at very fine scales (e.g., from burrow system to burrow system).

Although we systematically surveyed the colony and limited disturbance, we acknowledge that methodological factors might have influenced our assessment of predator effects. Spatial avoidance of predators, or similarities in space use of ferrets and predators, might not be detectable at the population level, or within our grid system, or might exist at another site within or outside the Conata Basin. Also, the locations we collected might not accurately estimate space use of coyotes or badgers; detectability of these species via spotlight might be biased (MacKenzie 2006). Our investigation of predator-effects was exploratory, spatial in nature, and limited to two mammalian predators of ferrets. Additional research is needed to evaluate the utility of monitoring these predators via spotlight surveys on colonies. Given that predation is often the main source of ferret mortality (Forrest et al. 1988, Biggins 2000, Biggins et al. 2006a, Breck et al. 2006), spotlighters should record observations of predators, including species other than coyotes and badgers, and perhaps prey other than prairie dogs (e.g., rabbits hunted by coyotes, Biggins 2000), at ferret reintroduction sites (USFWS 2006).

Resource connectivity indices also were not retained in our RSF models. Alternative connectivity indices or scales of assessment might be needed to evaluate influences of resource connectivity on resource selection of ferrets. We suspect, as previously proposed for other mustelids (e.g., *M. frenata*, Gehring and Swihart 2003), that ferrets "view patches and strips of good habitat within a landscape as havens of safety in a hostile sea" (King and Powell 2007:190). Influences of resource connectivity, if existent, likely vary within and across colonies of *Cynomys* species. When active burrows are more clustered, such as on white-tailed prairie dog colonies, connectivity of active burrows might influence ferret resource selection. Also, when burrow activity is generally low (vs. 86% herein), connectivity of all open burrows might influence ferret resource selection; patches of inactive burrows might provide corridors between patches of active burrows.

Conservation and management implications.–Black-footed ferrets selected areas with high active burrow abundance (see also Jachowski 2007, Livier 2007); ferrets might also select areas of high refuge density in general (Biggins et al. 2006c). Thus conservation and restoration of prairie dog colonies (Truett et al. 2006, Long et al. 2006, Proctor et al. 2006) of high burrow and prairie dog density are needed to promote continued recovery success. Such actions would also aid in conservation of prairie dogs, keystone species of the American prairie ecosystem (Kotliar 2000, Kotliar et al. 1999, 2006, Miller et al. 1994b), and additional associated species.

Accumulating evidence, here and elsewhere (Biggins et al. 2006c, Jachowski 2007), regarding fine-scale resource selection by ferrets suggests utility in assessing the fine-scale distribution of open and active burrows when evaluating potential black-footed ferret habitat. Current habitat evaluations involve coarse-scale consideration of these variables, indirectly for prairie dog prey (Biggins et al. 1993, 2006d, 2006e, Johnson and Collinge 2004). Resource selection models could complement coarse-scale habitat evaluations by providing a method of evaluating habitat suitability within colonies. Although a recent resource utilization function (RUF) model (Jachowski 2007) performed satisfactorily under evaluation via independent data (Chapter One), and our RSFs performed well under cross-validation, each model requires ground-mapping of prairie dog burrows, which might not be feasible when evaluating expansive sites. When ground-truthing is feasible, however, managers could utilize these models; our RSFs should be validated via independent data before use (Shifley et al. 2009). A more efficient method of burrow mapping is needed (e.g., satellite imagery mapping, Davis et al. 2008). When such a method is developed, RSFs and RUFs could supplant the coarse-scale approach to habitat evaluation, and aid in evaluating fine-scale habitat suitability at large scales.

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Table 1. Description of predictor variables considered when examining resource selection of 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, USA, 13 June through 10 October 2007, and 11 June through 27 September 2008.

Variable	Description
Open burrow	Number of black-tailed prairie dog burrows in cell
Open burrow contiguity	Black-tailed prairie dog burrow contiguity index of cell
Active burrow	Number of active black-tailed prairie dog burrows in cell
Active burrow contiguity	Active black-tailed prairie dog burrow contiguity index of cell
Edge	Euclidean distance from center of cell to edge of the prairie dog colony
Badger	Number of American badger locations in cell
Coyote	Number of coyote locations in cell

Table 2. Negative binomial 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, USA, 13 June through 10 October 2007, and 11 June through 27 September 2008. Parameters are listed with estimates (β), standard errors (*SE*), lower and upper Wald's 95% confidence intervals (CI), chi-square (χ^2) test statistics, and probability values ($\Pr > \chi^2$).

			Wald's 95% CI			
Variable	β	*SE*	Lower	Upper	χ^2	$\Pr > \chi^2$
2007						
Intercept	-9.4503	0.3850	-10.0724	-8.8282	886.49	<.0001
Active burrow	0.0265	0.0086	0.0201	0.0329	65.95	<.0001
Edge	0.0103	0.0057	0.0063	0.0143	25.85	<.0001
Active burrow × Edge	-0.0001	0.0000	-0.0001	0.0000	18.46	<.0001
Dispersion	1.5116	0.2945	1.0609	1.9624		
2008						
Intercept	-8.1042	0.2600	-8.4758	-7.7325	1826.61	<.0001
Active burrow	0.0162	0.0062	0.0124	0.0200	69.73	<.0001
Dispersion	2.3159	0.4074	1.6689	2.9630		

Table 3. Spearman-rank correlations (r_S) from cross-validation of models of black-footed ferret (*Mustela nigripes*) resource selection on the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, South Dakota, USA, 13 June through 10 October 2007, and 11 June through 27 September 2008. Correlations were conducted between frequencies of predicted resource selection function scores for test data and categories of resource selection function scores (bins). Bin size = 10 for the 2007 model and 18 for the 2008 model.

Set	2007		2008	
	r_S	*P*-value	r_S	*P*-value
1	0.9605	<.0001	0.9689	<.0001
2	0.9152	0.0002	0.8761	<.0001
3	0.9605	<.0001	0.9337	<.0001
4	0.9273	0.0001	0.9300	<.0001
5	0.9573	<.0001	0.9643	<.0001

Figure 5. Spatial distribution of black-tailed prairie dog (*Cynomys ludovicianus*) burrows in the South Exclosure, a 452-ha colony in the Conata Basin (inset map), Buffalo Gap National Grasslands, South Dakota, USA. Density of dot-stippling indicates open burrow density; lines indicate the colony edge. We monitored space use of 26 adult black-footed ferrets (*Mustela nigripes*) inhabiting the colony (5 monitored during both seasons), and collected locations of American badgers (*Taxidea taxus*) and coyotes (*Canis latrans*), 13 June through 10 October 2007, and 11 June through 27 September 2008.

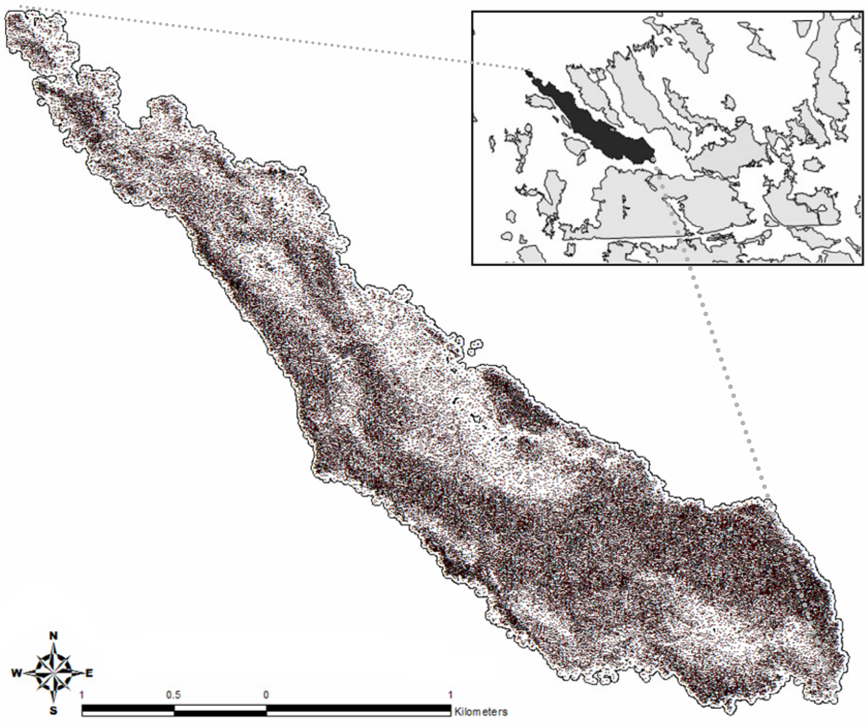


Figure 6. Global Moran's I statistic, a measure of colony-wide spatial autocorrelation of counts of open (solid line) and active (dashed line) black-tailed prairie dog *(Cynomys ludovicianus)* burrows in grid-system cells, versus square cell sizes (by meter) of incremental grid-systems overlain on a burrow map of the South Exclosure, a 452-ha prairie dog colony in the Conata Basin of southwestern South Dakota, USA. The distance at which Moran's I levels off (80 m, dotted line) indicates the grid-system in which spatial autocorrelation of open or active burrows was first minimized. We used the 80 × 80 m grid-system to evaluate fine-scale resource selection of black-footed ferrets (*Mustela nigripes*), 13 June through 10 October 2007, and 11 June through 27 September 2008.

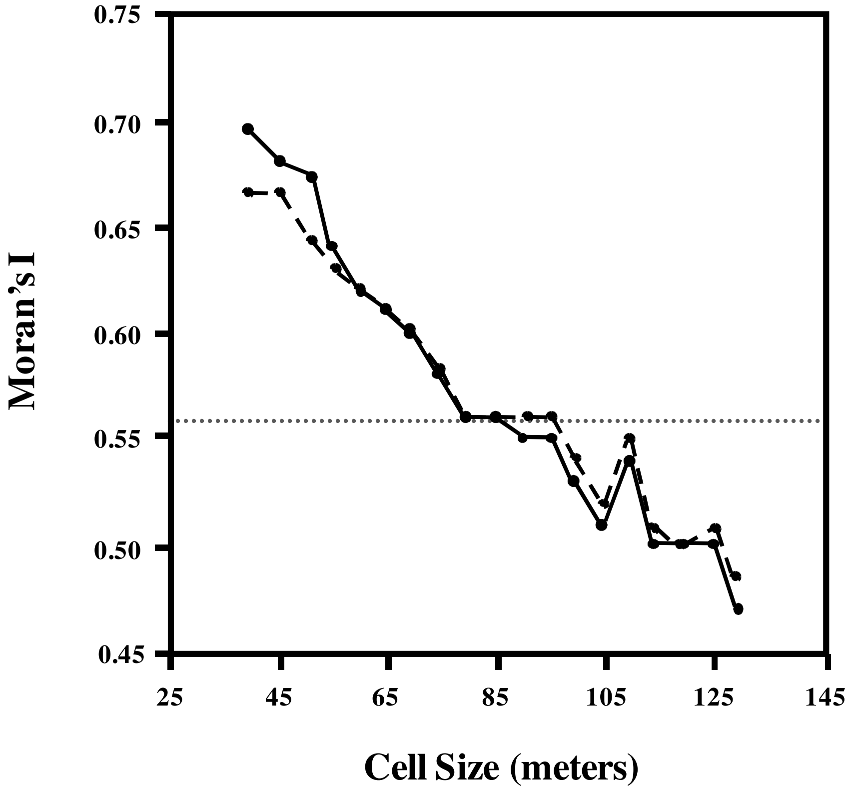
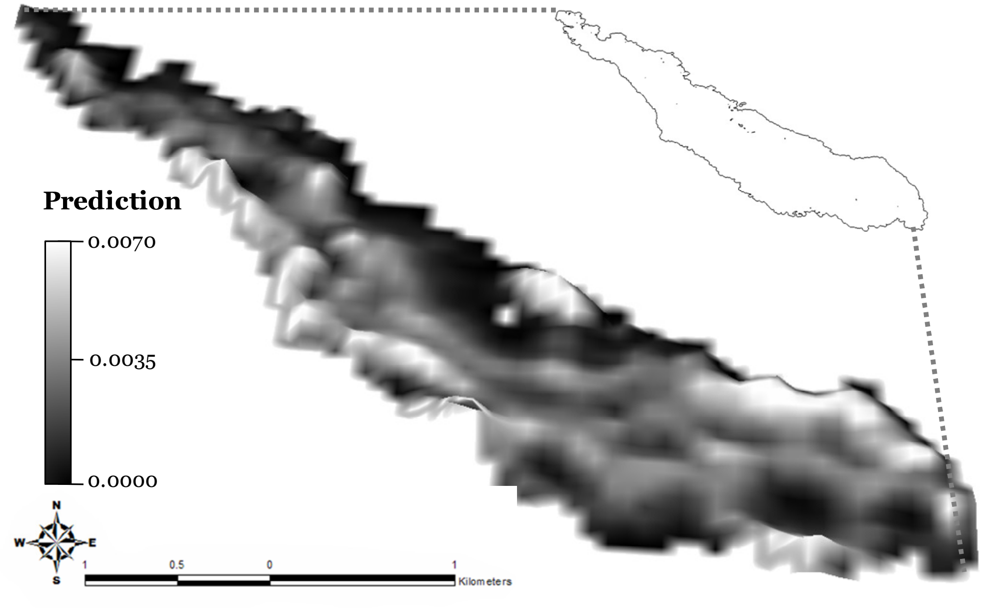


Figure 7. A interpolated, 3-dimensional surface of the estimated influence of active burrow counts in grid-cells (Active burrow), Euclidean distance from grid-cell centers to the nearest colony edge (Edge), and an interaction (Active burrow × Edge) upon predicted resource selection (Prediction) of black-footed ferrets (*Mustela nigripes*) on the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, Buffalo Gap National Grasslands, South Dakota, USA, 13 June through 10 October 2007. Ferrets selected areas of high active burrow abundance at colony edges (see also Fig. 5).



APPENDIX A: Identification numbers (first 2 numbers indicate confirmed or estimated year of birth; for instance, 02 = 2002) and number of spotlight survey observations of 12 adult black-footed ferrets (*Mustela nigripes*) observed between 13 June and 10 October 2007, on the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, Buffalo Gap National Grasslands, South Dakota, USA. Consecutive observations were separated by ≥ 12 hrs. The dye-marked female and male were each marked in early June.

		Animal ID	Number of Observations
2007	Females	02-001	45
		04-014	45
		05-006	38
		05-010	37
		05-046	43
		05-136	47
		06-016	12
		06-125	44
		Dye-marked	38
	Males	03-117	38
		05-158	38
		Dye-marked	33

APPENDIX B: Identification numbers and number of spotlight survey observations of 14 adult black-footed ferrets (*Mustela nigripes*) observed between 11 June and 27 September 2008, on the South Exclosure, a 452-ha black-tailed prairie dog (*Cynomys ludovicianus*) colony in the Conata Basin, Buffalo Gap National Grasslands, South Dakota, USA. Consecutive observations were separated by ≥ 12 hrs. The dye-marked male was marked in early June.

		Animal ID	Number of Observations
2008	Females	04-014	2
		05-006	20
		05-044	13
		05-046	35
		05-183	35
		06-125	39
		07-001	7
		07-015	55
		07-016	31
	Males	05-158	34
		07-010	30
		07-034	37
		07-047	43
		Dye-marked	37