ECOLOGICAL RELATIONSHIPS OF BLACK-FOOTED FERRETS, AMERICAN BADGERS, AND BLACK-TAILED PRAIRIE DOGS IN SOUTH DAKOTA

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AUTHORIZATION TO SUBMIT DISSERTATION

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ABSTRACT

Black-footed ferrets (*Mustela nigripes*) and American badgers (*Taxidea taxus*) co-exist in prairie dog (*Cynomys* spp.) ecosystems in North America. Ferrets are a federally-endangered mustelid that preys almost exclusively on prairie dogs and uses prairie dog burrows as shelter. Although badgers are morphologically specialized to excavate and prey on burrowing rodents, they often consume a diversity of vertebrates (primarily mammals), invertebrates, and plant material, and they sometimes kill ferrets. Black-tailed prairie dogs (*C. ludovicianus*) are stout, colonial ground squirrels that are often recognized as ecosystem engineers and as a keystone species in the grassland ecosystems of North America. We examined some of the ecological relationships among these three species at 2 study sites in South Dakota from 2008 to 2010. We documented asymmetric patterns of avoidance of badgers by ferrets based on the sex of both species. Female ferrets avoided adult female badgers, but not male badgers, and male ferrets exhibited less avoidance than female ferrets. Additionally, avoidance decreased with increasing densities of prairie dogs. Our results suggest that intersexual differences in space use by badgers creates varying distributions of predation risk that are perceived by the smaller carnivore (ferrets), and that females respond more sensitively than males to that risk. The positive association between security and food resources likely reduces the need for ferrets to trade off productive but risky habitats for less productive, safer ones. In our study, reproduction by prairie dogs was strongly influenced by precipitation received during the previous year and winter severity. Harsh winter conditions resulted in a marked decline in reproduction during one of the years of our study. In contrast, reproduction by ferrets varied little across years of our study, despite a marked decrease in the reproduction of prairie dogs during one year. Lastly, despite badgers often being characterized as generalists, we provide evidence of local specialization; badgers in our study behaved as prairie dog specialists. Badgers selected for prairie dog colonies and for areas of prairie dog colonies that had high densities of prairie dog burrows. On multiple scales, badgers in our study exhibited a narrow use of resources in comparison to the resources available. The common thread of our study was the influence of prairie dogs on the ecology of 2 native carnivores. Without adequate conservation, the functional role of prairie dogs in the grassland ecosystem as a keystone species will be diminished; thus the conservation of prairie dog colonies will benefit not only prairie dogs, but also badgers, ferrets, and other species associated with the prairie dog – grassland ecosystem.

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DEDICATION

For myself, my family, and my Tribe.

Above all, I dedicate this to my mother Wanda A. Clarke, and my grandparents, H. John and Arlene R. Grassel for instilling in me the love of land and animals.

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DISSERTATION INTRODUCTION

Black-footed ferrets (*Mustela nigripes*) and American badgers (*Taxidea taxus*) co-exist in prairie dog (*Cynomys* spp.) ecosystems in North America. Ferrets are a federally-endangered mustelid that preys almost exclusively on prairie dogs and uses prairie dog burrows as shelter (Sheets et al. 1972, Campbell et al. 1987, U. S. Fish and Wildlife Service 2013). Historically, their distribution coincided with the distributions of the black-tailed prairie dog (*C. ludovicianus*), Gunnison's prairie dog (*C. gunnisoni*), and white-tailed prairie dog (*C. leucurus*), which collectively occupied approximately 40 million ha of intermountain and prairie grasslands (Biggins et al. 1997, Clark 1986, Ernst et al. 2006). The decline of the ferret is a direct result of its close association with prairie dogs. From the late 1800s to approximately 1960, both prairie dog numbers and habitat were dramatically reduced by the effects of habitat conversion, lethal control, and disease, and as a result the ferret population declined precipitously (Biggins 2006).

The ferret was presumed extinct until a population was discovered near Meeteetse, WY, in 1981 (Clark et al. 1986, Lockhart et al. 2006). Following a disease outbreak at Meeteetse, all surviving wild black-footed ferrets were removed from the wild to initiate a captive breeding program (U. S. Fish and Wildlife Service 2013). The extant population today, both captive and wild, descends from 7 “founder” animals (U. S. Fish and Wildlife Service 2013). Efforts to reintroduce ferrets in the wild began in 1991 in the Shirley Basin, WY (Biggins 2006) and continue today. Current threats to the recovery of black-footed ferrets include susceptibility to disease (sylvatic plague) and loss of habitat and prey base stemming from the direct mortality of prairie dogs due to disease (sylvatic plague) and the use of toxicants (U. S. Fish and Wildlife Service 2013).

Ferrets co-exist on prairie dog colonies with American badgers, another carnivorous mustelid that preys on prairie dogs and sometimes preys on ferrets (Biggins et al. 1999, 2006, 2011). Unlike ferrets, badgers are not dependent on prairie dogs but their association with burrowing rodents and other prey that require grasslands or shrubsteppe has resulted in steep population declines in some areas where suitable habitats have been considerably reduced [e.g., Washington (Washington Department of Fish and Wildlife 2005), California (Williams 1986)]. Badgers are a species of conservation concern in several states and listed as a species-at-risk in Canada (Committee on the Status of Endangered Wildlife in Canada 2012). While the size and shape of ferrets allow them to easily move through most burrows of prairie dogs, badgers, which are nearly 8 times larger than ferrets, excavate burrows to acquire prairie dogs. The potential for competition between the two carnivores is likely high due to overlap in both habitat use and diet.

Black-tailed prairie dogs are stout, colonial ground squirrels that are often recognized as ecosystem engineers and as a keystone species in the grassland ecosystems of North America (Miller et al. 1994, 2000, Kotliar et al. 1999, Davidson et al. 2012). Prairie dog colonies create discrete patches of short vegetation with highly conspicuous, clustered burrow systems, which attract and are used by variety of uniquely adapted species (Miller et al. 1994, Kotliar et al. 1999). Populations of black-tailed prairie dogs have declined by approximately 98% since historical accounts (Miller et al. 2000), and they were considered a candidate for federal protection from 2000 to 2004 (U. S. Fish and Wildlife Service 2004). The loss of large, contiguous blocks of prairie dog habitat has been detrimental to the recovery of black-footed ferrets. In recent years, ferret reintroductions have occurred on fragmented prairie dog complexes that support relatively small colonies because few large prairie dog complexes remain (Forrest 2005, Proctor et al. 2006, Jachowski and Lockhart 2009). Competitive interactions, including intraguild predation, can be amplified in fragmented landscapes (Creel 2001), which could have a profound effect on efforts to re-establish ferret populations in their native habitat.

Although there has been considerable research conducted on ferrets, badgers, and prairie dogs, most have been studies of a single species or studies that have involved prairie dogs and either ferrets or badgers. The primary goals of this endeavor were to better understand some of the ecological relationships that exist among ferrets, badgers, and prairie dogs and to improve our understanding of the role each species plays in the ecosystem. In Chapter 1, we investigated spatial interactions between different sex and age categories of ferrets and badgers. We also evaluated how the density of prairie dogs and size of prairie dog colonies might influence this relationship. In Chapter 2, we evaluated several factors that might influence the productivity of prairie dogs. Because ferrets are so inextricably linked with prairie dogs, we also examined how the productivity of prairie dogs might influence the productivity of ferrets. In Chapter 3, we investigated patterns of selection by badgers at multiple scales to test the hypothesis that badgers would exhibit behaviors more closely aligned with specialists than generalists when inhabiting landscapes with prairie dogs. With this work, we not only improved our understanding of the ecology of 3 prairie wildlife species that individually have been the focus of regional and national conservation efforts, but we also improved our understanding of a unique ecosystem.

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CHAPTER 1: SPATIAL INTERACTIONS BETWEEN SYMPATRIC CARNIVORES: ASYMMETRIC AVOIDANCE OF AN INTRAGUILD PREDATOR

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ABSTRACT

Interactions between intraguild species that act as both competitors and predator-prey can be especially complex. We studied patterns of space use by the black-footed ferret (*Mustela nigripes*), a prairie dog (*Cynomys* spp.) specialist, and the American badger (*Taxidea taxus*), a larger generalist carnivore that competes for prairie dogs and is known to kill ferrets. We expected that ferrets would spatially avoid badgers because of the risk of predation, that these patterns of avoidance might differ between sexes and age classes, and that availability of food and space might influence these relationships. We used location data from 60 ferrets and 15 badgers to model the influence of extrinsic factors (prairie dog density and colony size) and intrinsic factors (sex, age) on patterns of space use by ferrets in relation to space use by different sex and age categories of badgers. We documented asymmetric patterns of avoidance of badgers by ferrets based on the sex of both species. Female ferrets avoided adult female badgers, but not male badgers, and male ferrets exhibited less avoidance than female ferrets. Additionally, avoidance decreased with increasing densities of prairie dogs. We suggest that intersexual differences in space use by badgers creates varying distributions of predation risk that are perceived by the smaller carnivore (ferrets), and that females respond more sensitively than males to that risk. This work advances understanding about how competing species coexist and suggests that including information on both intrinsic and extrinsic factors might improve our understanding of behavioral interactions between sympatric species.

INTRODUCTION

Interactions between sympatric taxa help shape the structure of ecological communities because they can influence the demography, distribution, and behavior of species within communities (Holt and Polis 1997, Berger and Gese 2007). When sympatric species use similar resources, interspecific interactions are likely to include 1 of 2 forms of competition (Linnell and Strand 2000). Exploitative competition occurs when 1 species is more efficient than its competitors at exploiting available resources (Case and Gilpin 1974). Alternatively, interference competition occurs when less efficient competitors directly interfere with their more specialized competitors, which can result in the direct displacement of competitors (Case and Gilpin 1974), kleptoparasitism (Creel 2001, Creel et al. 2001), or intraguild predation (Polis et al. 1989, Palomares and Caro 1999). The latter can be a significant source of mortality for some species, and such interactions are of particular concern when threatened or endangered species are killed by competitors (Palomares and Caro 1999, Linnell and Strand 2000).

The potential for competition between sympatric carnivores using similar resources is largely determined by the extent of spatial overlap (Kitchen et al. 1999, Palomares and Caro 1999, Sergio et al. 2003). Therefore, to minimize interference competition and the risk of intraguild predation, the strategy of a subordinate competitor often includes avoidance of the dominant species (Case and Gilpin 1974, Robinson and Terborgh 1995, Atwood and Gese 2010). Among mammalian carnivores for example, red foxes (*Vulpes vulpes*) avoid coyotes (*Canis latrans*) by establishing home ranges outside of the areas used by coyotes (Major and Sherburne 1987, Theberge and Wedeles 1989). Bobcats (*Lynx rufus*) also avoid interactions with coyotes at fine spatial scales by establishing core use areas that do not overlap with coyote core areas (Thornton et al. 2004). Similarly, home ranges of coyotes often are located along the edges of wolf (*Canis lupus*) territories or in the matrix between territories of neighboring wolf packs (Arjo and Pletscher 1999). Availability of spatial refugia can be important for coexistence of competitors, including intraguild prey and predators (Sergio et al. 2003).

Within Mustelidae, there are several sympatric species with similar niches that have developed mechanisms to co-exist. Mink (*Mustela vison*) and river otters (*Lutra canadensis*) persist in coastal marine environments by partitioning diets and also habitat by the amount of wave action and over-story cover (Ben-David et al. 1995). Similar results were reported for mink and Eurasian otters (*Lutra lutra*) co-existing in riverine environments (Bonesi and Macdonald 2004, Bonesi et al. 2004). In North America, short-tailed weasels (*M. erminea*) reduce use of their preferred habitat when occupied by long-tailed weasels (*M. frenata*), a dominant guild member that has been documented to kill and eat short-tailed weasels (Gamble 1980, St-Pierre et al. 2006). In Europe, the least weasel (*M. nivalis*) and short-tailed weasel co-exist because the subordinate least weasel can avoid confrontations with the dominant generalist by using the tunnels and runways of voles (*Microtus* spp.), its primary prey (King and Moors 1979, Aunapuu and Oksanen 2003).

Similarly, black-footed ferrets (*M. nigripes*; hereafter ferrets) and American badgers (*Taxidea taxus*; hereafter badgers) co-exist in prairie dog (*Cynomys* spp.) ecosystems in North America. Ferrets are obligate specialists that are dependent on prairie dogs for food and reside within burrows created by prairie dogs (Biggins 2006). In contrast, badgers are often considered generalist foragers that are common in a variety of grassland-dominated habitats where they consume a diversity of vertebrates (primarily mammals), invertebrates, and plant material (Messick and Hornocker 1981, Lampe 1982, Goodrich and Buskirk 1998, Sovada et al. 1999). When available, prairie dogs often are the most common food item in the diet of badgers (Goodrich and Buskirk 1998), and both ferrets and badgers select areas with high densities of active burrows where prairie dogs are relatively abundant (Biggins et al. 1993, Jachowski et al. 2011, Eads et al. 2011, 2013). Overlap in diet and fine-scale patterns of resource selection likely results in strong competition between the 2 carnivores. Badgers are known to kill ferrets (Biggins et al. 1999, 2006a, 2011b) and excavate prairie dog burrows more often in areas recently used by a ferret, suggesting that badgers actively hunt ferrets, steal prey from ferrets, or both (Eads et al. 2103).

We evaluated the influence of intrinsic factors (sex and age) and extrinsic factors (prairie dog density and prairie dog colony size) on space use by ferrets in relation to space use by badgers. First, we hypothesized that ferrets would reduce the potential for intraguild predation by spatially avoiding badgers. We predicted that 1) adult female badgers would have the greatest influence on space use by ferrets because female badgers are more attuned to the distribution of prey resources and have smaller territories than males (Messick and Hornocker 1981, Minta 1993, Goodrich and Buskirk 1998), and thus, female badgers likely create a more predictable presence that intraguild prey might attempt to avoid; 2) female ferrets, which are about half the size of male ferrets (Anderson et al. 1986), would avoid badgers more than males because of increased vulnerability to predation and a need to minimize the risk of predation on neonates; and 3) adult ferrets would exhibit greater avoidance of badgers than juvenile ferrets because social dominance allows adults to select areas with lower risk. Second, we hypothesized that availability of food (prairie dogs) would influence space use by ferrets, and we expected that ferrets would trade off increased risk of predation by badgers for access to food by exhibiting less spatial avoidance of badgers when densities of prairie dogs were relatively low. Finally, we hypothesized that the availability of spatial refugia would influence space use by ferrets, and we predicted that ferrets occupying small colonies would exhibit less spatial avoidance of badgers relative to ferrets on large colonies because the lack of space would prevent ferrets from maintaining safe distances from areas of high use by badgers.

However, because badgers select the same habitat patches as ferrets and might be attracted to ferrets (Eads et al. 2013), our alternate hypothesis was that at fine spatial scales, ferrets and badgers would occupy space concurrently. Coexistence of ferrets and badgers at fine spatial scales would likely be facilitated, in part, by the relatively high efficiency of ferrets to prey on prairie dogs as compared to badgers (i.e., exploitative competition) and by the selection of burrow systems with multiple openings, which likely lowers the risk of predation by badgers (Biggins 2012). Understanding factors that shape spatial interactions between generalists and specialists that have overlapping niches can provide insight into the function and structure of biotic communities.

STUDY AREA

We conducted our study from 2008 to 2010 on 2 native prairie grasslands, the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, located approximately 250 km apart in central and southwestern South Dakota, USA, respectively. At the Lower Brule Indian Reservation, our research was conducted on the Fort Hale Bottom prairie dog complex (469857E, 4868645N NAD 83 Zone 14N; hereafter Lower Brule) located in a fragmented mixed-grass prairie dominated by western wheatgrass (*Pascopyrum smithii*), green needlegrass *(Nassella viridula*), buffalo grass (*Bouteloua dactyloides*), and needle-and-thread (*Hesperostipa comata*). The area is primarily used for livestock grazing but cultivated agriculture also is common. In 2007, the Lower Brule study site contained 25 prairie dog colonies totaling 642.5 ha (range = 0.1 – 209.1 ha, $\bar{x}$ = 23.8). Our research focused on 6 prairie dog colonies that ranged in size from 9.3 to 207.7 ha ($\bar{x}$ = 53.8 ha). Previous work using visual count methods (Severson and Plumb 1998) estimated densities of prairie dogs at 44.7/ha and 56.1/ha in 2004 and 2005, respectively (Lower Brule Sioux Tribe *unpublished data*). This population of ferrets was established when captive-born and wild-born ferrets were translocated from captive breeding facilities and other recovery sites in 2006 and 2007. During our study, the ferret population was comprised primarily of wild-born offspring and a few wild-born ferrets from the original releases.

Our research at the Buffalo Gap National Grasslands occurred on the Heck Table prairie dog complex (699205E, 4843996N NAD 83 Zone 13N; hereafter Buffalo Gap). The site is a mixed-grass prairie dominated by western wheatgrass, buffalograss, blue grama (*Bouteloua gracilis*), and prickly pear cactus (*Opuntia polyacantha*), and it is nearly devoid of tree and shrub species (Schroeder 2007, Livieri and Anderson 2012). Primary land uses for the area are cattle grazing and recreation (Livieri and Anderson 2012). In 2007, the Buffalo Gap study site supported 31 colonies of prairie dogs that totaled 1192.9 ha (range = 0.2 – 284.6 ha, $\bar{x}$ = 38.5 ha). Our research focused on 2 colonies that were 250.3 and 284.6 ha in size. Densities of prairie dogs were estimated at 27.9/ha in this area in 1999 (Biggins et al. 2011a) and 41.0/ha on nearby colonies in the Conata Basin in 2007 (Biggins et al. 1993, Eads et al. 2011). This population of ferrets was established in 1999 with the release of ferrets reared at captive breeding facilities and wild-born ferrets translocated from the Conata Basin. During our study, all ferrets were wild-born.

METHODS

Ferret and badger monitoring. –We located ferrets for capture and marking and for subsequent relocations by conducting night-time spotlight surveys (Biggins et al. 2006b), which consisted of an observer in a vehicle using a roof-mounted spotlight to search prairie dog colonies for the reflective eye-shine of ferrets. At Lower Brule, we captured ferrets using wire cage traps (91.5 x 10 x 10 cm) placed into burrow entrances, anesthetized individuals in a mobile laboratory setting using isoflurane, and implanted each with Passive Integrated Transponders (PIT; AVID® Microchip I.D. Systems, Folsom, Louisiana, USA). A contractor for the U. S. Forest Service marked ferrets at Buffalo Gap. Ferrets detected visually during subsequent surveys were identified using automated PIT tag readers placed at the opening of the burrow (Fagerstone and Johns 1987, Stoneberg 1996, Biggins et al. 2006b), and their locations were recorded using handheld GPS receivers. Individuals that anesthetized ferrets received specialized training and authorization from the U. S. Fish and Wildlife Service (permit #TE-131398).

We searched prairie dog colonies to locate badgers for capture. We set padded leg-hold traps (#3 coil spring, Victor Soft Catch, Woodstream Corp., Lititz, Pennsylvania, USA) at the entrance of occupied badger burrows. Trapped individuals were chemically immobilized with an intramuscular injection of ketamine hydrochloride and xylazine hydrochloride (15 mg/kg body weight and 1.5mg/kg, respectively; Goodrich and Buskirk 1998), marked with a PIT, and fitted with a harness-style radio-transmitter weighing approximately 100 – 110g (Advanced Telemetry Systems, Isanti, Minnesota, USA). The anesthetic effects of xylazine hydrochloride were reversed by intravenous injection of yohimbine (0.125 mg/kg; Goodrich and Buskirk 1998). Relocations of telemetered badgers were primarily obtained at night.

We monitored ferrets and badgers year-round at Lower Brule and seasonally at Buffalo Gap. Monitoring of both species occurred during November 2008 – November 2010 at Lower Brule and May – November 2009 at Buffalo Gap. We considered juvenile badgers and ferrets independent of their parents on 1-September of the year of their birth and did not include locations of juveniles prior to this date in our analyses. Juveniles were considered adults on 1-April of the year after their birth.

Prairie dog colony size and density. –We mapped prairie dog colonies at Lower Brule in August 2007, and personnel of the U. S. Forest Service mapped colonies at Buffalo Gap during May – September 2007 using Trimble® GeoXM™ GPS receivers (1-m accuracy) while driving an ATV or walking along the perimeters of the colonies. Edges of colonies were distinguished by the distinct difference in vegetation height caused by foraging and vegetation clipping behavior of black-tailed prairie dogs (Koford 1958, Hoogland 1995). We imported data into ArcGIS (v. 9.3, ESRI, Redlands, California, USA) to estimate colony size and to conduct spatial analyses.

We captured and marked prairie dogs to estimate relative densities at the colony level. We conducted trapping within randomly selected 0.5-ha plots during June – July 2008 at the Lower Brule site, June 2009 at both study sites, and also during June 2010 at the Lower Brule site. At Lower Brule, we established 4 trapping plots on each of 6 prairie dog colonies, which resulted in sampling 1 – 22% of the area of each colony. At Buffalo Gap, we established 12 plots on the smaller colony (250.3 ha) and 16 on the larger colony (284.6 ha), which resulted in sampling 2 – 3% of each colony. Each plot contained 61 wire box traps (Tomahawk Livetrap Company, Tomahawk, Wisconsin, USA; Tru-Catch Traps, Belle Fourche, South Dakota, USA) baited with grain and molasses pellets spaced 10 m apart in a 7x7 design with 12 additional traps placed in areas with high densities of burrow openings to minimize trap saturation. We pre-baited plots for 3 days prior to trapping, and we set and checked traps twice each day for 4 consecutive days and checked them once on the 5th day (i.e., 9 trapping sessions). We marked prairie dogs on initial capture with hair dye in 2008, by clipping a toe-nail in 2009, and by clipping a toe-nail and applying individually-numbered ear tags in 2010. An index of relative density for each colony was obtained each year by averaging the total number of individuals marked per plot across all plots. We attempted to improve these estimates using accumulation curves and modifications to Peterson-Lincoln estimation methods (Schnabel 1938, Chapman 1951), but these methods produced unrealistic estimates. Therefore, we used the average number marked per plot to provide a relative index of density of prairie dogs on the study colonies rather than an estimate of population density. All animal use methods were approved by the University of Idaho Animal Care and Use Committee (protocol #2008-26) and conformed to the guidelines for use of wild mammals in research established by the American Society of Mammalogists (Sikes et al. 2011).

Spatial analyses. –Our study design followed a second order selection analysis of habitat use versus availability (Johnson 1980). We buffered all ferret locations with an 80-m-radius circular plot to represent areas used by ferrets, and we generated 3 random locations per ferret location, which were cast outside of the buffered use areas but within the prairie dog colony where that ferret was located. If a ferret used >1 colony, which did not occur often, the number of random locations included for each colony was proportional to the number of ferret relocations per colony.

We generated utilization distributions (UDs) for each badger to estimate the relative intensity of use across space (Van Winkle 1975, Kernohan et al. 2001). We used fixed-kernel estimation (Worton 1989) with a likelihood cross-validation smoothing parameter to estimate individual 99% UDs with a grid cell size of 30 x 30 m using the Hawth's Tools extension (Beyer 2004) in ArcGIS and Animal Space Use (v. 1.3, Horne and Garton 2009). We estimated UDs for each badger for which we recorded ≥27 locations. For juvenile badger UDs, we only used locations collected between 1-September of their birth year and 31-March of the following year. For badgers that were radio-tracked as juveniles and adults, a juvenile and adult UD were created when there were an adequate number of locations for each age category.

We determined a value for intensity of badger use for both random and available ferret locations by extracting the raster value from overlapping badger UDs in ArcGIS. If a location was within the UD of >1 badger, we summed the values for intensity of badger use and developed cumulative estimates for adult female badgers, adult male badgers, and all badgers.

Statistical analyses. –We evaluated relative support for models of intrinsic and extrinsic factors shaping space use by ferrets relative to intensity of space use by badgers. We modeled characteristics predicting used and unused sites with logistic regression with a repeated measure on individual ferrets to control for individual variability using the GENMOD procedure in SAS (v. 9.3, SAS Institute Inc., Cary, North Carolina, USA). We used sex and age of each ferret as intrinsic predictor variables and colony-level attributes (colony size and relative density of prairie dogs) as extrinsic predictor variables. We included the effect of study site in some models because features unique to each study site (e.g., other predators, alternative prey, etc.) that we did not measure also might influence spatial interactions between ferrets and badgers.

Our primary focus was evaluation of spatial interactions, and consequently, we modeled the probability of use by ferrets in relation to the space use by badgers. Our candidate models included the intrinsic and extrinsic predictor variables and their 2-way interactions with the variable that represented intensity of badger use. Interactions between the intensity of badger use and colony-level attributes (colony size and relative density of prairie dogs) would be a consequence of how badgers use prairie dog colonies, which would vary spatially across colonies. To determine if sex or age categories of badgers influenced ferrets differently, we developed a set of models for adult female badgers, adult male badgers, and all badgers. Each set contained 12 candidate models that included the effects of study site, sex and age of the ferret, relative density of prairie dogs, size of prairie dog colonies, and the variable for relative intensity of badger use. Each set of models only differed by the variable that represented the intensity of badger use (i.e., adult females, adult males, or all badgers). The effect of badger presence was modeled as interactions with the other variables, and consequently, must be interpreted in relation to the other variables. We compared models using quasilikelihood under the independence model criterion (QIC; Pan 2001, Burnham and Anderson 2002, Hardin and Hilbe 2003) to identify the most parsimonious models that fit the observed data.

RESULTS

We recorded 707 locations from 15 badgers ($\bar{x}$ = 47.1, range = 27 – 84, SD = 21.0): 6 adult females, 1 juvenile female, 4 adult males, 3 juvenile males, and 1 female that was radio-tracked as a juvenile and as an adult. We recorded 639 locations from 60 ferrets ($\bar{x}$ = 10.7, range 3 – 34, SD = 8.2): 16 adult females, 15 juvenile females, 11 adult males, 7 juvenile males, and 11 ferrets (4 females and 7 males) that had locations recorded as both juveniles and as adults. Our analyses included prairie dog colonies that ranged in size from 9.3 to 284.6 ha (n = 8, $\bar{x}$ = 107.1 ha, SD = 119.9 ha), and indices of relative densities of prairie dogs that averaged 9.0 to 66.5 per 0.5-ha plot (n = 17 colony years, $\bar{x}$ = 29.3, SE = 3.7).

As expected, adult female badgers more strongly influenced space use by ferrets than other sex and age categories. Only 2 of the candidate models evaluating space use by ferrets were included in the 95% confidence set (i.e., models with $\geq$ 95% of the weight, W_i, based on the QIC values), and both included intensity of use by adult female badgers rather than adult males or all badgers (Table 1-1). Models with other sex and age categories of badgers were >133 ΔQIC from the top model and received < 0.0001 percent of the model weight, indicating markedly poorer fits to the data.

Both intrinsic and extrinsic factors shaped the spatial interactions of ferrets and badgers. Patterns of avoidance of adult female badgers differed between the sexes of ferrets and were influenced by the relative density of prairie dogs. As we predicted, female ferrets exhibited stronger spatial avoidance of adult female badgers than males. Both candidate models in the 95% confidence set included sex of ferrets and relative density of prairie dogs, each interacting with the intensity of use by adult female badgers (Table 1-1). Parameter estimates from the top model with >94% of the model weight, indicated that both of these factors were significant, and that avoidance of badgers by female ferrets was nearly twice that of males (Table 1-2). Ferrets spatially avoided badgers on colonies with lower densities of prairie dogs, but contrary to our expectations, avoidance decreased with increasing densities of prairie dogs (Figure 1-1).

The top model also included the variable for the interaction between study site and intensity of use of adult female badgers, suggesting that patterns of avoidance of adult female badgers by ferrets differed between study sites (Table 1-1). However, the parameter was not significant in that model ($P = 0.199$), suggesting that differences between study sites had a relatively weak influence on avoidance of badgers by ferrets in comparison to ferret sex and relative density of prairie dogs.

Neither the size of prairie dog colonies nor the age class of ferrets appeared to have a marked effect on spatial interactions between ferrets and badgers in our study. Although colony size was in 1 model in the 95% confidence set (Table 1-1), the parameter was not significant ($P = 0.774$), and the model was not considered a competing model (ΔQIC = 6.19).

DISCUSSION

Our results revealed complex, asymmetric patterns of spatial overlap between 2 sympatric carnivores that interact as potential competitors and as potential prey and predators. As expected, badgers did not influence space use by ferrets equally across sex and age categories; adult female badgers had a greater influence on the movements of ferrets than adult male badgers or all badgers combined. Ferret response to badgers likewise differed between sexes, with females responding more strongly than males. These differences suggest that the spatial interactions of sympatric species might be difficult to predict without information about how intrinsic factors shape behavioral interactions among individuals.

One explanation for the difference in apparent influence of female and male badgers on space use by ferrets is that intersexual differences in space use result in spatially concentrated versus dispersed predation risk. Badgers exhibit distinct intersexual differences in social behavior and space use: female spatial organization is shaped largely by the distribution of food resources while male spatial patterns are determined primarily by the distribution of females, which results in the territories of females being smaller than those of males (Messick and Hornocker 1981, Minta 1993, Goodrich and Buskirk 1998). Adult female badgers preferentially use prairie dog colonies when available, establish their territories within colony boundaries, and prey primarily on prairie dogs (Goodrich and Buskirk 1998). Within prairie dog colonies, adult female badgers might be considered an "organizing force" and the core area of their territory may create an "influence field" that intraguild prey might attempt to avoid (Forman 1995). This relationship has been in observed in other predator-prey systems. For example, eagle owls (*Bubo bubo*) are considered to have an organizing force on black kites (*Milvus migrans*), which minimize their predation risk by establishing territories outside of the influence of owl pairs (Sergio et al. 2003). Similarly, the presence of tiger sharks (*Galeocerdo cuvier*), even at low densities, influenced the spatial patterns of bottlenose dolphins (*Tursiops aduncus*), such that dolphins avoid using areas that were used by tiger sharks even though food was abundant (Heithaus and Dill 2002). Wolf packs can influence spatial patterns of both potential prey and intraguild competitors. White-tailed deer (*Odocoileus virginianus*; Mech 1977), elk (*Cervus elaphus;* Fortin et al. 2005), and coyotes (Arjo and Pletcher 1999) minimize risk of predation by avoiding areas used by wolves. In our study, the more restricted pattern of space use that characterizes adult female badgers likely creates a predator presence that is more predictable in space and time relative to males, and ferrets can likely detect and respond more readily to this relatively static cue of predation risk.

Spatial responses of intraguild prey in our study differed between the sexes, with female ferrets exhibiting greater avoidance of badgers than males. Female ferrets are potentially more vulnerable to predation than male ferrets because they are nearly half the size of males (Anderson et al. 1986), and females raising young might be especially vulnerable; dens of maternal females frequently contain prey provisioned for offspring, and badgers are attracted to burrows containing dead prairie dogs (Biggins 2000). Similar to badgers, ferrets exhibit intersexual differences in social behavior and spacing patterns; female ferrets maintain smaller territories than males (Forrest et al. 1985, Jachowski et al. 2010, Livieri and Anderson 2012), presumably because females are focused on food resources and males are controlling access to potential mates (Powell 1979, Miller et al. 1996).

The smaller territory sizes of female ferrets likely results in less frequent overlap and decreased potential for encounters with badgers relative to that experienced by male ferrets. A lower probability of engaging with intraguild predators likely decreases the probability of predation (Moehrenschlager et al. 2007). Sex-biased avoidance of predators by females with young is common in mammals [e.g., moose (*Alces alces*, Oehlers et al. 2011); bighorn sheep (*Ovis canadensis*, Berger 1991); cheetahs (*Acinonyx jubatas*, Durant 2000)], and indeed, anti-predator behaviors have been documented to shape maternal behavior in other intraguild predator-prey systems (Waltzer and Schausberger 2011, Wen-San and Pike 2012). When establishing territories, female ferrets likely select for areas that minimize the risk of predation to young and also for areas that provide adequate prey.

Availability of food resources also influenced spatial interactions between intraguild predators and prey in our study system. We expected that avoidance of badgers by ferrets would decrease as densities of prairie dogs declined because ferrets would accept higher risks of predation in exchange for access to adequate food resources (e.g., Lima and Dill 1990, Thompson and Gese 2007, Wilson et al. 2010), however, our results suggested an opposite trend. Both sexes of ferrets avoided badgers when prey densities were relatively low, and both sexes exhibited less avoidance at relatively high prey densities; however, female ferrets maintained greater avoidance of badgers over a wider range of prey densities when compared with males (Figure 1-1). Decreased competition might explain why ferrets exhibited less avoidance of badgers as densities of prairie dogs increased. Hyper-abundant food resources can relax interference competition and facilitate co-existence between 2 competitors (Holt and Polis 1997). Perhaps badgers exhibit less aggressive behavior towards ferrets when prairie dogs are abundant, and ferrets might respond by decreasing spatial avoidance. Although this relationship has not been well documented among carnivores, the abundance of food was suspected to lower competition and contribute to the tolerance of red fox by coyotes in Yellowstone National Park (Gese et al. 1996). Similarly, the amount of food eaten by dominant carnivores greatly influenced the level of tolerance exhibited toward other carnivores in Africa (Kruuk 1972, Schaller 1972).

Greater density of prairie dogs not only increases the amount of available food for ferrets, but the concomitant increase in prairie dog burrows also would lower risk of predation by badgers because of increased availability of refuges. Prey typically responds to predator presence by increasing use of refuges (Sih et al. 1988). Our results support a conclusion by Biggins et al. (2006c) that the positive association between security and food resources likely reduces the need for ferrets to trade off productive but risky habitats for less productive, safer ones.

Contrary to our expectations, age did not strongly influence models of space use by intraguild prey. We expected adult ferrets to exhibit greater avoidance of badgers than juveniles because other research has suggested a social hierarchy in this species (Forrest et al. 1988, Livieri and Anderson 2012, Biggins et al. 2006a). Perhaps social hierarchies in ferrets exist to provide control of food resources (by females) and mating potential (by males) more than avoidance of predators; future research could investigate this hypothesis.

We also expected that ferrets occupying smaller colonies would exhibit less spatial avoidance of badgers than ferrets on larger colonies because increased availability of space often is associated with lower predation risk in traditional and intraguild predator–prey systems (Suhonen 1993, Sergio et al. 2003, Kotler et al. 2004, Morrison et al. 2010). Our results did not support this prediction, however, our research focused on 2 colonies that were large (250.3 and 284.6 ha) at Buffalo Gap and 6 colonies that varied in size (9.3 to 207.7 ha) at Lower Brule; therefore, the variable for prairie dog colony size was likely confounded with study site, which was a non-significant parameter in our top model. Many other aspects that could influence spatial behavior of ferrets and badgers differed between the study sites, including surrounding habitat, alternative prey, predator community, proximity to roads, and other human activity. Consequently, our data might not have permitted a rigorous test of the effect of colony size on spatial interactions between badgers and ferrets.

Our results rely on a couple of important assumptions. One assumption is that we accurately characterized areas used by badgers. The number of locations used to estimate UDs for some badgers is slightly lower than 30, the number typically suggested to estimate the home range of an organism (Seaman et al. 1999). The UDs for 5 of 15 badgers were estimated with 27 – 29 locations. However, the remaining 10 badger UDs were estimated with 32 – 84 locations ($\bar{x}$ = 57). Second, we assumed that ferrets spatially avoided badgers rather than the opposite. Theoretically, the spatial patterns we described could be attributed to avoidance of ferrets by adult female badgers, perhaps because ferrets are superior at exploitative competition. Although this explanation is plausible, we believe that the more likely explanation for the space use patterns we documented is avoidance of badgers by ferrets to reduce risk of intraguild predation by badgers. Not only are badgers up to 8 times heavier than ferrets (Anderson et al. 1986, Minta 1992), but they are known to kill ferrets (Biggins et al. 1999, 2006a, 2011b).

Our alternative hypothesis – that ferrets and badgers would occupy space concurrently at fine spatial scales – was only supported when interactions between adult female badgers and ferrets occurred at relatively high density of prairie dogs. These results might appear to contradict recent research suggesting that badgers concentrate their activities in areas frequently used by ferrets and that they actively pursue ferrets (Eads et al. 2013). Several issues, however, hinder direct comparisons between these studies. First, our study used locations of individually marked animals, and consequently, we were able to determine differences in patterns of spatial interactions by sex and age categories. Second, radio transmitters on badgers in our study permitted collection of locations when individuals were active above ground and resting below ground, while Eads et al. (2013) only used locations of badgers above ground. Different space use patterns are likely to emerge when locations are obtained from animals engaged in differing activities and behaviors. Third, the studies differ in scale. Within a relatively short temporal scale, badgers might selectively excavate burrows in areas used by ferrets (Eads et al. 2013), but over longer time periods, our study revealed that some ferrets (females) are able to spatially avoid some badgers (adult females). We suggest that the conclusions of this study and Eads et al. (2013) are both valid, and that differences are due, in part, to activity of badgers when locations were collected, scale, and most importantly, the use of marked individuals. In our study, failing to account for sex would have obscured relationships that structure spatial interactions, and the asymmetric patterns of avoidance of badgers exhibited by ferrets would have been missed.

Our study has several implications for understanding spatial interactions between other sympatric species. First, we documented complex patterns of avoidance in an intraguild predator-prey system, but these patterns would likely have been undetectable if the sex of both predators had not been considered explicitly. Second, intersexual differences in patterns of space use also likely shaped spatial interactions between the species by creating differences in distribution of predation risk. Because reproductive strategies of males and females often result in sex-specific patterns of space use, this factor is likely to shape spatial interactions in many ecological systems. Third, density of food resources influenced observed spatial interactions between the 2 intraguild competitors, which suggests that the strength and direction of interactions will vary over space and time with extrinsic factors. These results support the need for interpreting spatial relationships in the context of both intrinsic and extrinsic influences on sympatric species.

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Table 1-1. Ninety-five percent confidence set of the candidate models of factors influencing probability of space use by black-footed ferrets relative to space use by badgers on colonies of black-tailed prairie dogs within the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008-2010.

Model	QIC[a]	ΔQIC[b]	W_i[c]
AFB Sex PD Site AFB*Sex AFB*PD AFB*Site	1935.95	0	0.947
AFB Sex PD Colony AFB*Sex AFB*PD AFB*Colony	1942.14	6.19	0.043

[a] QIC is the quasilikelihood under the independence model criterion

[b] ΔQIC is the difference from the model with the lowest QIC value

[c] W_i is the QIC weight of the model

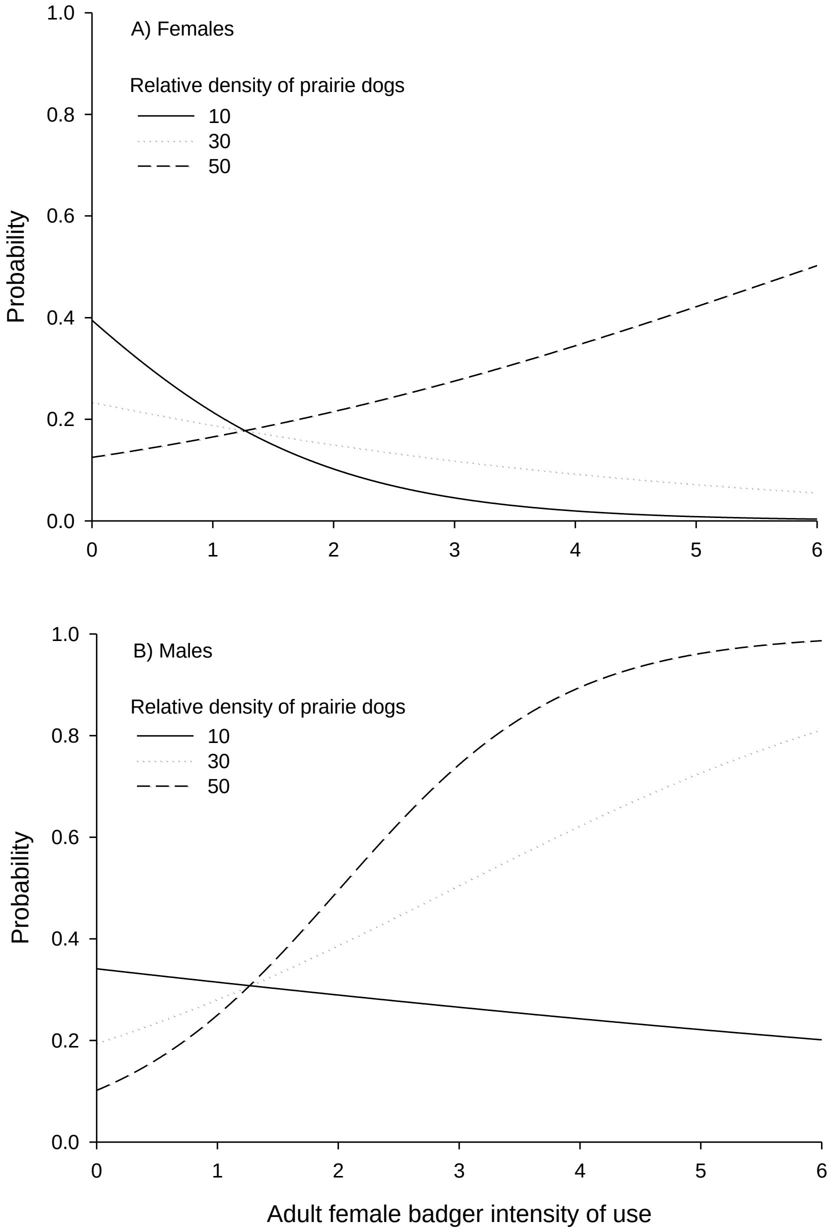
Variables for models: adult female badger intensity of use (AFB), ferret sex (Sex), relative prairie dog density (PD), colony size (Colony), and study site (Site). Two-way interactions are denoted by an asterisk.

Table 1-2. Parameter estimates for the top model evaluating space use by black-footed ferrets relative to space use by badgers on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008 – 2010.

Parameter	Coefficient Estimate	Standard Error	95% Confidence Limits		*P* value
Intercept	-0.279	0.379	-1.022	0.463	0.461
AFB	-0.420	0.597	-1.589	0.748	0.482
Sex (F)	0.232	0.141	-0.045	0.508	0.101
PD	-0.038	0.014	-0.066	-0.010	0.008
Site (BG)	-0.549	0.294	-1.126	0.027	0.062
AFB*Sex (F)	-0.754	0.282	-1.308	-0.201	0.008
AFB*PD	0.030	0.013	0.004	0.055	0.024
AFB*Site (BG)	1.267	0.986	-0.666	3.200	0.199

Variables for models: adult female badger intensity of use (AFB), ferret sex (Sex), relative prairie dog density (PD), colony size (Colony), and study site (Site). Two-way interactions are denoted by an asterisk.

Figure 1-1. Probability of space use by female (A) and male (B) black-footed ferrets (*Mustela nigripes*) as a function of relative intensity of use by adult female badgers (*Taxidea taxus*) and relative density of black-tailed prairie dogs (*Cynomys ludovicianus*). The lines representing prairie dog densities ranging from 10 to 50 individuals per 0.5-ha plots were within the range of variation documented across our study sites. Adult female badger intensity of use is an index that was within the range of variation documented across our study sites. Sex of ferrets and relative density of prairie dogs were both significant factors (Table 1-2).



CHAPTER 2: REPRODUCTION BY BLACK-TAILED PRAIRIE DOGS AND BLACK-FOOTED FERRETS: EFFECTS OF CLIMATE AND FOOD AVAILABILITY

In review: Grassel, S. G., J. L. Rachlow, and C. J. Williams. Reproduction by black-tailed prairie dogs and black-footed ferrets: effects of climate and food availability. Journal of Mammalogy.

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ABSTRACT

Food availability is one of the most important factors influencing reproduction in mammals; however, reproductive success of some species can be negatively affected when body reserves are depleted during long periods of adverse climatic conditions. We investigated the relationship between forage availability, climatic variables, reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*), and reproduction by black-footed ferrets (*Mustela nigripes*), a prairie dog specialist predator. Prairie dogs draw on stored energy reserves to support reproduction (i.e., capital breeding), while ferrets likely rely on availability of prey during the reproductive period (i.e., income breeding). We expected that productivity of prairie dogs would positively correlate with precipitation during the previous summer and availability of spring forage, and that harsh winter conditions would negatively affect reproduction. We also expected that productivity of ferrets would be positively correlated with productivity of prairie dogs because of the net increase in available prey during the litter-rearing season of ferrets and because female ferrets might selectively prey on juvenile prairie dogs. At 2 sites in South Dakota during 2008 – 2010, reproduction by prairie dogs was strongly influenced by precipitation received during the previous year and winter severity. Harsh winter conditions resulted in a marked decline in reproduction during 2010. Although reproduction by ferrets varied little across years of our study, long-term conservation and reintroduction strategies for the endangered black-footed ferret could be influenced by climate-driven changes in reproduction by prairie dogs.

INTRODUCTION

Food availability is one of the most important environmental factors influencing reproduction in mammals, acting both as a proximate and an ultimate cause of annual variation in reproductive output (Bronson 1989). Animals that use energy stored from food consumed prior to the breeding season to support reproduction are considered capital breeders (Drent and Daan 1980, Houston et al. 2007), and individuals with larger energy reserves upon initiation of reproduction tend to have greater reproductive success (Prop and Black 1998). In contrast, income breeders immediately use energy from food to support reproduction (Drent and Daan 1980, Houston et al. 2007) and generally exhibit weak correlations between body condition and reproductive success (Andersen et al. 2000, Boyd 2000). Across mammals, breeding strategies fall along a capital-income continuum, and many species exhibit a mixed strategy whereby animals rely on a combination of capital and income resources throughout their reproductive periods (Thomas 1988, Jönsson 1997, Drent 2006).

For capital breeders, body reserves can provide an energetic buffer against challenging environmental or nutritional conditions that might occur during winter and early spring (Fauchald et al. 2004), but rates of depletion of reserves can be influenced by harsh winter weather (Stewart et al. 2005, Parker et al. 2009). Adverse winter conditions can negatively influence the nutritional status of female ungulates in north temperate regions (Adams 2005, Garroway and Broders 2005), resulting in smaller offspring at birth (Adams 2005, Couturier et al. 2009), delayed parturition, postnatal growth, and development (Rachlow and Bowyer 1991, Adams 2003), and reduced neonatal survival (Adams et al. 1995, Hamel et al. 2010). Likewise, reproductive success of smaller mammals also can be influenced by severe winter conditions. For example, prolonged snow cover decreased litter size and frequency of reproduction in yellow-bellied marmots (*Marmota flaviventris*; Van Vuren and Armitage 1991). Similarly, reproduction by Columbian (*Urocitellus columbianus*) and Belding's (*U. beldingi*) ground squirrels was negatively affected by late winter and early spring snowstorms (Morton and Sherman 1978, Neuhaus et al. 1999). Indeed, frequency and duration of severe winter conditions can be important drivers of population dynamics in many mammal species (Gaillard et al. 2000, Patterson and Power 2002).

Prairie dogs (*Cynomys* spp.) are colonial ground squirrels that rely on energy reserves gained during the autumn for reproduction during the subsequent spring. The primary factor affecting their reproductive success (defined as the number of juveniles that emerge from natal burrows) is the body mass of adult females (Hoogland 2001), which is closely associated with the quantity and quality of available forage (Wright-Smith 1978, Garrett et al. 1982, Rayor 1985, Travis and Slobodchikoff 1993, Hoogland 1995, Cully 1997). Body mass of female black-tailed prairie dogs (*C. ludovicianus*) during autumn was positively correlated with body mass during the next breeding season, and heavier females had higher reproductive success (Hoogland 1995). In addition, litter sizes of black-tailed prairie dogs counted *in utero* were positively correlated with precipitation received during the previous summer (Knowles 1987), which also suggests that forage availability during the previous growing season influenced reproductive success. These relationships suggest that on the capital-income breeding continuum, prairie dogs appear to be most closely associated with capital breeders. However, if prairie dogs use a mixed strategy, which is typical of most species that rely on capital resources during reproduction (Mainguy and Thomas 1985, Meijer and Drent 1999, Bowen et al. 2001, Gauthier et al. 2003, Fletcher et al. 2013), then availability of forage during lactation also likely influences reproductive success.

Black-footed ferrets (*Mustela nigripes*) prey primarily on prairie dogs and are probably like other small mustelids, which store little body fat and show little seasonal variation in accumulation of fat (Sheets et al. 1972, Campbell et al. 1987, Buskirk and Harlow 1989, Harlow 1994). Limited fat reserves likely provide a benefit in maintaining the long, slim body shape required for fossorial activity (Brown and Lasiewski 1972). Consequently, on the capital-income continuum, ferrets are likely to be categorized as income breeders, meaning that availability of prey during the reproductive period likely influences reproductive success. Young prairie dogs are especially important prey items to many predators including black-footed ferrets (Clark 1976, Hoogland 1981, Halpin 1983, Loughry 1987, Brickner et al. 2014). Recent research has suggested that adult female ferrets might focus predation on juvenile prairie dogs while raising young (Brickner et al. 2014), which suggests a functional link between the reproductive success of ferrets and prairie dogs.

We investigated relationships between seasonal forage availability, climatic variables, reproduction of prairie dogs, and reproduction of ferrets. First, we hypothesized that productivity of prairie dogs would positively correlate with precipitation during the previous summer as well as availability of spring forage during the current year, and that harsh winter conditions would negatively affect reproduction. We used estimates of each of these variables at two study sites to model relationships between predictors and an index of prairie dog reproduction. Second, we hypothesized that productivity of ferrets would be positively correlated with productivity of prairie dogs because of the net increase in available prey during the litter-rearing season of ferrets and because female ferrets might selectively prey on juvenile prairie dogs. We used 2 indices of ferret reproduction at one of two study sites to qualitatively examine this relationship.

Understanding the effects of climatic conditions on reproductive success of prairie dogs is important to their long-term conservation and the conservation of associated species. Prairie dogs serve as ecosystem engineers and often are recognized as a keystone species in the grassland ecosystems of North America (Miller et. al 1994, 2000, Kotliar et al. 1999, Davidson et al. 2012). Black-footed ferrets are extreme specialists that depend on prairie dogs for food and use their burrows for shelter (Sheets et al. 1972, Campbell et al. 1987, Biggins 2006). A better understanding of factors that influence reproductive success of both prairie dogs and ferrets will assist managers in evaluating potential recovery strategies and reintroduction sites for black-footed ferrets, which are a federally-endangered mammal (U. S. Fish and Wildlife Service 2013). Furthermore, knowledge about how climate influences the dynamics of the prairie dog and black-footed ferret system can facilitate integration of changing climate regimes into conservation strategies for both species.

STUDY AREA

We conducted our study on two native prairie grasslands, the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, located approximately 250 km apart in central and southwestern South Dakota, USA, respectively. At the Lower Brule Indian Reservation, our research was conducted on the Fort Hale Bottom prairie dog complex (469857E, 4868645N NAD 83 Zone 14N; hereafter Lower Brule) located in a fragmented mixed-grass prairie dominated by western wheatgrass (*Pascopyrum smithii*), green needlegrass *(Nassella viridula*), buffalograss (*Bouteloua dactyloides*), and needle-and-thread (*Hesperostipa comata*). The area is primarily used for livestock grazing but cultivated agriculture also is common. Black-footed ferrets were reintroduced to this site beginning in 2006 (U. S. Fish and Wildlife Service 2013).

Our research at the Buffalo Gap National Grasslands occurred on the Heck Table prairie dog complex (699205E, 4843996N NAD 83 Zone 13N; hereafter Buffalo Gap). The site is a mixed-grass prairie dominated by western wheatgrass, buffalograss, blue grama (*Bouteloua gracilis*), and plains pricklypear cactus (*Opuntia polyacantha*), and it is nearly devoid of tree and shrub species (Schroeder 2007, Livieri and Anderson 2012). Primary uses for the area are cattle grazing and recreation (Livieri and Anderson 2012). Ferrets were reintroduced to this site beginning in 1999 (Biggins et al. 2011).

METHODS

Prairie dog reproduction. –We captured and marked prairie dogs to develop a relative index of the ratio of juvenile:adult prairie dogs to characterize annual reproductive success. We conducted trapping within randomly selected 0.5-ha trapping plots during June – July 2008 and June 2009 at both study sites and also during June 2010 at the Lower Brule site. At Lower Brule, we established 4 trapping plots on each of 7 prairie dog colonies that ranged in size from 9.3 – 207.7 ha ($\bar{x}$ = 58.1 ha), which resulted in sampling 1 – 22% of the area of each colony. At Buffalo Gap, we established trapping plots on 2 prairie dog colonies and the number of plots was proportional to the size of the prairie dog colony; we sampled 3% of each colony with 16 plots on the larger colony (284.6 ha) and 12 plots on the smaller one (213.5 ha). Each plot contained 61 wire cage traps (Tomahawk Livetrap Company, Tomahawk, Wisconsin; Tru-Catch Traps, Belle Fourche, South Dakota) baited with grain and molasses pellets spaced 10 m apart in a 7x7 design with 12 additional traps placed in areas with high densities of burrow openings to minimize trap saturation. We pre-baited plots for 3 days prior to trapping, and we set and checked traps twice each day for 4 consecutive days and checked them once on the 5th day (i.e., 9 trapping sessions). We marked prairie dogs on initial capture with hair dye in 2008, by clipping a toe-nail in 2009, and by clipping a toe-nail and applying individually-numbered ear tags in 2010. To develop a relative index of reproductive success, we averaged the number of juvenile and adult prairie dogs captured on trapping plots within each prairie dog colony and expressed these calculations as a ratio.

Because ferret presence can influence numbers of prairie dogs on colonies, we classified whether or not colonies were occupied by female ferrets with litters during the summer or autumn seasons (*sensu* Biggins et al. 2012). Female ferrets raising litters have elevated energetic requirements, resulting in higher rates of predation on prairie dogs (Biggins et al. 1993), and consequently, should have a greater effect on the attributes of prairie dog populations than females without litters or male ferrets. We did not attempt to estimate ferret densities. Unoccupied colonies were those where female ferrets with litters were not detected.

Ferret reproduction. –We developed 2 indices to characterize the annual reproductive success of ferrets at the Lower Brule study site. We recorded the number of juvenile offspring observed with adult female ferrets during summer and autumn spotlight surveys to estimate litter size (Biggins et al. 2006). We also estimated the ratio of juvenile:adult females captured and marked during spotlight surveys conducted during September – October of each year. Night-time spotlight surveys were conducted from a vehicle with a roof-mounted spotlight during which we searched prairie dog colonies for the reflective eye-shine of ferrets (Biggins et al. 2006). At Lower Brule, we captured ferrets using wire cage traps (91.5 x 10 x 10 cm) placed into burrow entrances, anesthetized individuals in a mobile laboratory setting using isoflurane, and implanted each with Passive Integrated Transponders (PIT; AVID® Microchip I.D. Systems, Folsom, Louisiana). We recorded the sex and age class (juvenile or adult) of each ferret; adults were distinguished from juveniles by measuring the width of the upper canine teeth and by tooth coloration (Santymire et al. 2012). A contractor for the U. S. Forest Service marked ferrets at Buffalo Gap. All procedures were approved by the University of Idaho Animal Care and Use Committee (Protocol #2008-26) and are consistent with American Society of Mammalogists guidelines for the use of wild mammals in research (Sikes et al. 2011). Individuals that anesthetized ferrets received specialized training and authorization from the U. S. Fish and Wildlife Service (permit #TE-131398).

Climate variables. –We obtained climate data (temperature, average daily wind speed, snow depth, and precipitation) from the nearest automated weather stations to each study site (South Dakota Office of Climatology 2013). We calculated a prairie dog winter severity index (PDWSI) for each study site using the number of days with a maximum wind chill index of ≤-12.0 °C and the number of days with ≥13.0 cm of snow on the ground following an approach employed in other studies (e.g., Brinkman et al. 2005, Grovenburg et al. 2011). The wind chill index was calculated using the average daily wind speed and maximum daily temperature and was used instead of ambient temperature because wind can result in a substantial increase in heat loss (Bakken 1981) and reduced aboveground activity of prairie dogs (Severson and Plumb 1998). We calculated winter severity scores from 1 November – 15 March by assigning 1 point for each day that the wind chill index or snow depth exceeded thresholds and 2 points for each day when both conditions exceeded thresholds. We categorized these values as mild (PDWSI < 40), moderate (PDWSI = 40 – 80), and severe (PDWSI > 80) and treated these as ordinal, categorical variables in our analyses.

We obtained precipitation data during the previous year's growing season for each study site. In northeastern Montana, *in utero* litter sizes of prairie dogs were correlated with the amount of precipitation received during June – September of the previous year (Knowles 1987). Because our study sites are located in at more southerly latitudes where the growing season is longer, we used total precipitation that occurred during May – October of the previous year in our analyses (South Dakota Office of Climatology 2013).

Forage availability. –To evaluate the influence of food on the reproductive success of prairie dogs, we estimated an index of available forage on prairie dog colonies during the current year's growing season. We visually stratified colonies by plant community (forb or grass) and grouped colonies by general soil association units (U. S. Department of Agriculture 2006) to account for variability in vegetative productivity associated with these variables. A total of 24, 1-m^2 plots per study site were randomly located within prairie dog colonies, distributed across strata in proportion to the area of colonies within each strata at each study site. Exclosures were placed around the plots in mid-May of each year, and after approximately 5 weeks, vegetation within the exclosures was clipped at the ground surface, dried at 40^{o} C for 24 hours, and weighed to estimate biomass of potential forage. Exclosures were constructed of expanded metal (4 sides and top cover) and approximately 30 cm in height, and prevented all herbivores (e.g., prairie dogs, livestock) from grazing in plots.

Statistical analyses. –We modeled factors that potentially influence reproductive success of prairie dogs with a mixed linear model that included a repeated measure on colony using the MIXED procedure in SAS (v. 9.3, SAS Institute Inc., Cary, North Carolina, USA). We constructed a set of 11 *a priori* candidate models (Table 2-1) representing multiple hypotheses and evaluated them using an information theoretic approach, with models ranked via Akaike's information criterion adjusted for small sample size (AICc; Burnham and Anderson 2002). Models within ΔAICc $\leq$2 of the best model were considered competing models. We calculated Akaike weights (w_i), the probability that the *i*th model is the best approximating model among all candidate models, and determined the 95% confidence set of models (Burnham and Anderson 2002). For models within the 95% confidence set, we calculated the relative importance weights for each parameter.

RESULTS

Reproduction by prairie dogs varied across years in a similar pattern at both study sites, Reproduction was markedly higher in 2009 than in 2008 and was lowest at the Lower Brule site during 2010. At Lower Brule, the relative index of juveniles to adults captured per colony (n = 7) averaged 0.56 juveniles:adults (range = 0.30 – 0.86) in 2008, 0.97 (range = 0.32 – 1.20) in 2009, and 0.20 (range = 0.05 – 0.42) in 2010 (Table 2-2). At Buffalo Gap, the index on the 2 colonies that we monitored was 0.56 juveniles:adults (range = 0.39 – 0.66) in 2008 and 0.81 (range = 0.73 – 0.84) in 2009 (Table 2-2).

Estimates of available forage on prairie dog colonies varied markedly across years at the Lower Brule site, but less so at the Buffalo Gap study site. Dry weight biomass of potential forage at Lower Brule averaged 70.9 g/m^2 across 3 strata (range = 56.8 – 96.4 g/m^2) during 2008, which was

1.5 times greater than the 2009 estimate and 2 times higher than the 2010 estimate (Table 2-2). In contrast, available forage estimates were more similar between years at the Buffalo Gap study site (average = 56.8 g/m^2 across 2 strata in 2008 and 44.5 g/m^2 in 2009).

Precipitation received during the previous year varied moderately among years, but values in all years were above long-term seasonal averages for both study sites. The Lower Brule site received 40.0, 49.0, and 42.4 cm of precipitation during May – October in 2007, 2008, and 2009, respectively, which was slightly above the long-term (1971 – 2006) average of 36.8 cm (South Dakota Office of Climatology 2013). A similar pattern of precipitation occurred at the Buffalo Gap site during our study; an estimated 33.7 and 48.7 cm of precipitation occurred during May – October of 2007 and 2008, respectively, and the long-term average was 31.7 cm (South Dakota Office of Climatology 2013). In contrast to summer-fall precipitation, winter conditions varied considerably between study sites. At Lower Brule, winters were mild, moderate, and severe in 2007 – 2008, 2008 – 2009, and 2009 – 2010, respectively, but winter conditions at Buffalo Gap were classified as mild during both years of our study.

Reproduction by prairie dogs was strongly influenced by precipitation received during the previous year and winter severity during our study. The top-ranked model included both of these variables, had 61% of the Akaike weight (w_i), and was 4.7 times more likely (w_{best}/w_i) to be the best explanation for variation in reproduction by prairie dogs than the next best supported model (Table 2-3). The second model, which contained the variable for winter severity only, had a ΔAICc $\geq$ 3.1, and thus was not considered a competing model. Additionally, all five models in the 95% candidate set (except the null model) included either precipitation received during the previous year or winter severity. One model in the candidate set also included the variable for presence of ferrets, and none included the variable for forage availability, suggesting that these latter parameters had less influence on reproduction by prairie dogs during our study.

Prairie dog reproduction was negatively affected by severe winter conditions and positively affected by precipitation received during the previous summer-fall growing season, and both of these parameter estimates were significant (Table 2-4). The relative importance value (R_i) for winter severity ($R_i = 0.82$) was higher than previous year's rain ($R_i = 0.64$), suggesting that harsh winter conditions had a greater effect on reproduction by prairie dogs during our study than the influence of rainfall during the previous growing season. Inclusion of the null model with a ΔAICc of 3.2 in our 95% candidate set, however, suggests that the effects of the significant variables in the top model (previous year's rain and winter severity) were likely modest given our ability to detect an effect. At

Lower Brule, the previous year's rain increased 23% from 2008 to 2009, and the index of reproduction by prairie dogs increased by 61% between those years. During the same years at Buffalo Gap, precipitation increased 45%, and the index of reproduction by prairie dogs similarly increased by 50%. Winter conditions were characterized as mild and moderate during this period at Lower Brule and mild during both of these years at Buffalo Gap. In contrast, reproduction by prairie dogs at Lower Brule in 2010, the year of the severe winter, was 77% and 64% lower than in 2009 and 2008, respectively.

We observed no qualitative decrease in the relative reproductive success of ferrets following low reproduction by prairie dogs at the Lower Brule site. Observed litter size of ferrets averaged 3.7 (n = 7), 3.3 (n = 6), and 3.7 (n = 7) in 2008, 2009, and 2010, respectively, and during those years, with similar effort, we captured and marked 2.4, 2.5, and 3.0 juvenile ferrets per adult female. These data suggest that a consistent number of juvenile ferrets were born annually during this time period despite marked differences among years in reproduction by prairie dogs.

DISCUSSION

During our study, climatic conditions were the primary factors that affected reproduction by prairie dogs. Our results support previous research indicating that precipitation received during the previous year was a significant factor affecting *in utero* litter sizes of prairie dogs (Knowles 1987). Although other research has suggested that persistent snow cover and cold temperatures can delay breeding in prairie dogs (Knowles 1987), we could find no other reports of the substantial negative effects of harsh winter weather on their reproduction. Our research suggests that prairie dogs, like other capital breeders, can be markedly affected by climatic variation across multiple seasons, which could be important for long-term persistence of populations given changing precipitation and winter climatic conditions that are expected within the species' range.

Our results suggested that during mild and moderate winters, precipitation received during the previous summer-fall strongly influenced reproduction by prairie dogs. During our study, precipitation at both study sites was at or above average for all years. During Knowles' (1987) study, precipitation ranged from drought conditions to record high rainfalls, and prairie dog productivity in that study was correlated with those extremes. Abundant rainfall received at our study sites should have provided adequate food resources to support high prairie dog productivity during all years of our study. Although precipitation received during the previous year might have the greatest influence on the reproduction of prairie dogs during most years, the effects of severe winter conditions appeared to trump the positive effects of abundant precipitation during our study. We hypothesize that winter conditions likely have a threshold effect rather than an additive effect on the reproduction of prairie dogs; in our study, the negative effects of winter conditions were not evident until conditions were severe.

Prairie dogs in our study area are typically active year-round, but during one winter of our study they experienced severe cold and snowy weather that persisted for much of the winter season including early portions of the breeding season. Although aboveground activity of prairie dogs was not measured during our study, we noted a distinct lack of such activity for 3 – 4 months during the winter of 2009 – 2010. Until recently, black-tailed prairie dogs were not thought to hibernate during the winter (King 1955, Bakko 1977, Bakko et al. 1988, Hoogland 1995). However, evidence has more recently been published indicating that black-tailed prairie dogs exhibit a range of winter thermoregulation behavior, and that they can enter short, shallow bouts of facultative torpor induced by environmental conditions (Lehmer et al. 2001, 2003, Lehmer and Biggins 2005), as well as longer periods that constitute hibernation during severe drought conditions (Lehmer et al. 2006). Black-tailed prairie dogs at the northernmost extent of the species' range that typically experience harsh winter conditions on an annual basis will hibernate during winter and exhibit varied depths of torpor across years and among colonies, suggesting that annual and local variation in climate or microclimate influences torpor patterns (Gummer 2005). Based on our observations, we believe that the winter conditions in 2010 were severe enough to cause prairie dogs in our study area to enter a prolonged torpor or hibernation.

While capturing prairie dogs in 2010, we noted that many females were not lactating (i.e., had no visible teats), and those that were experienced delayed molting (many females were nearly hairless) and were in poor body condition (e.g., conspicuous rib and pelvic bones). These observations are noteworthy because when animals hibernate, periodic arousals occur during which body temperatures return to normal, and this can be energetically costly (Wang 1979). Animals that store fat to survive hibernation are limited in the number of arousals that occur (Thomas et al. 1990) and risk exhausting fat reserves if the number of arousal periods are excessive (Jonasson and Willis 2011, 2012). The high prevalence of non-lactating females in our populations suggested that many females were in poor condition and either did not breed or did so and reabsorbed embryos, which has been documented previously in prairie dogs (Foreman 1962, Knowles 1987). Furthermore, individual body condition can affect molting (Hollister 1916, Hoogland 1995) such that individuals in lower body condition molt later than those in better condition. Hoogland (1995) reported that lactating females typically have the lowest body condition and latest molting dates when compared to other prairie dogs. Our observations support the contention that prairie dogs during our study might have entered hibernation during harsh winter conditions, which likely negatively affected body condition and subsequent reproduction.

The lack of a strong effect of spring forage on prairie dog reproduction lends support to the assertion that prairie dogs are capital breeders that rely on resources acquired prior to the breeding season to support reproduction. It is also plausible that adequate rainfall might have resulted in adequate forage such that forage was not a limiting factor for reproduction during our study. Regardless, this variable had less of an influence on reproduction than either previous year's rain or winter severity. Our index of reproduction did not encompass the entire period of lactation, and more research is needed to better understand the importance of forage availability during the lactation and weaning periods on recruitment of prairie dogs into the breeding population.

Although there has been considerable debate about the effects of black-footed ferret predation on population dynamics of prairie dogs (Henderson et al. 1969, Hillman and Linder 1973, Biggins et al. 2012), the presence of maternal ferrets on prairie dog colonies did not strongly influence prairie dog reproduction during our study. We followed the approach of Biggins et al. (2012) and used a binary variable to indicate colonies that were occupied by a maternal ferret. A more robust analysis would evaluate the influence of ferret density; however, accurate estimates of ferret densities are difficult to obtain because of their semi-fossorial and elusive nature. As a consequence, our assessment of the effect of ferrets should be interpreted with caution.

Indices of the relative reproductive success of ferrets varied little across all years of our study at Lower Brule, despite a 77% decrease in reproduction of prairie dogs in 2010 from the previous year. We expected that reproduction by ferrets would correlate with fluctuations in reproduction by prairie dogs because of changes in prey availability during the litter-rearing phase of ferret reproduction, an effect that has been reported for other specialist mustelids (King 1983, King et al. 2003). Furthermore, our prediction would be bolstered if female ferrets selectively preyed on juvenile prairie dogs. Predators typically prey upon young or substandard individuals (Errington 1946, Slobodkin 1968, Curio 1976, Morse 1980), and juvenile prairie dogs (60-100 g at emergence) are likely easier for a female ferret to kill than an adult prairie dog (~1400 g), which weigh about two times more than a female ferret (Anderson et al. 1986, Hoogland 1995). Recent investigations of the diet of ferrets using stable isotopes indicated female ferrets selected for smaller prey relative to males, which suggests females might selectively prey on juvenile prairie dogs over adult prairie dogs

(Brickner et al. 2014). Although our qualitative data did not support our prediction, a quantitative comparison of the age structure of prairie dogs within populations and ferret kills would provide a critical test of this hypothesis.

Regional conservation strategies are increasingly including provisions for system responses to changing climate patterns (e.g., Browne and Humburg 2010, Schrag 2011), and our results suggest that these considerations should be incorporated into conservation planning for the prairie dog – ferret system. Changing climatic conditions could adversely affect prairie dogs in the northern Great Plains due to severe periodic reductions in forage availability caused by an increased frequency of drought (U. S. Global Change Research Program 2009, Schrag 2011). Hotter and drier summers coupled with severe winter weather could reduce viability of prairie dogs in some areas, and because black-footed ferrets are inextricably linked to prairie dogs, long-term conservation for this endangered mammal will likely benefit from considering actions to mitigate the effects of climate change on prairie dog populations.

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Table 2-1. Set of 11 *a priori* candidate models explaining reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008 – 2010.

Model	Variables
1	Null (intercept only)
2	Previous year rain
3	Previous year rain + ferret presence
4	Previous year rain + winter severity
5	Spring forage
6	Spring forage + ferret presence
7	Spring forage + previous year rain
8	Winter severity
9	Winter severity + ferret presence
10	Winter severity + previous year rain+ spring forage
11	Winter severity + spring forage

Notes: Variables for models: previous year rain (total rainfall from 1 May – 31 October), winter severity (the number of days with a maximum wind chill index of $\leq$-12.0 °C and the number of days with $\geq$13.0 cm of snow on the ground from 1 November – 15 March), ferret presence (prairie dog colonies with (1) or without (0) a maternal ferret), and spring forage (average biomass (g/m^2) available to prairie dogs May – June based on vegetation collected within plots).

Table 2-2. Reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*) and forage estimates used to model factors affecting prairie dog reproduction on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008 – 2010. Numbers of adults, juveniles, and juvenile:adult ratios are the mean values (±SE) of individuals captured within 1-ha live-trapping plots at each study site. Forage biomass is an estimate of forage available on prairie dog colonies at each site during May – June based on vegetation collected within plots.

	Lower Brule			Buffalo Gap	
	2008	2009	2010	2008	2009
Adults	15.6 (1.5)	21.5 (1.9)	20.0 (2.0)	3.8 (0.7)	8.6 (1.1)
Juveniles	8.7 (1.4)	20.9 (3.1)	3.9 (0.8)	2.1 (0.5)	7.0 (0.9)
Juvenile:Adult ratio	0.56 (0.07)	0.97 (0.11)	0.20 (0.05)	0.56 (0.16)	0.81 (0.26)
Forage Biomass (g/m^2)	70.9 (9.4)	47.5 (7.0)	35.0 (5.3)	56.8 (6.0)	44.5 (6.9)

Table 2-3. Ninety-five percent confidence set of candidate models of factors influencing reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008 – 2010.

Model	AICc	ΔAIC	w_i	Σw_i	w_{best}/w_i
Winter severity index + previous year rainfall	16.7	0	0.61	0.61	-
Winter severity index	19.8	3.1	0.13	0.74	4.7
Null	19.9	3.2	0.12	0.86	5.0
Winter severity index + ferret presence	20.8	4.1	0.08	0.94	7.8
Previous year rainfall	22.6	5.9	0.03	0.97	19.1

Notes: The Akaike Information criterion adjusted for small sample size (AICc), ΔAIC, Akaike weights (w_i), sum of Akaike weights (Σw_i), and evidence ratios (w_{best}/w_i) are reported for each model.

Table 2-4. Parameter estimates for the best supported model evaluating reproduction by black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, South Dakota, during 2008 – 2010.

Variable	$\hat{\beta}$ (SE)	95% CI
Previous year rain	0.0454 (0.0125)	0.019 to 0.072
Winter severity index	-0.227 (0.0663)	-0.370 to -0.085

CHAPTER 3. WHEN GENERALISTS BEHAVE AS SPECIALISTS: LOCAL SPECIALIZATION BY AMERICAN BADGERS

To be submitted. Grassel, S. G., and J. L. Rachlow. When generalists behave as specialists: local specialization by American badgers.

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ABSTRACT

Differentiating species according to their relative niche breadth is a common approach in community ecology that can result enhance understanding about how species relate to the environment. Although a species might have generalized ecologies across its entire range, on a local scale, individuals might function as specialists. American badgers (*Taxidea taxus*) are terrestrial carnivores that have been described most often as generalists. We compared patterns of habitat selection by badgers at 3 scales to test the hypothesis that badgers would exhibit behaviors more closely aligned with specialists than generalists when inhabiting landscapes with black-tailed prairie dogs (*Cynomys ludovicianus*). At a course scale, badgers selected for prairie dog colonies across the landscape. At an intermediate scale, we documented significantly greater use of prairie dog colonies within the home ranges of badgers. At fine scales within colonies, badgers used areas that had relatively high densities of prairie dog burrows, where prey was presumably abundant. On multiple scales, badgers exhibited a narrow use of resources in comparison to the resources available. Our study provides evidence that badgers behave as specialists when burrowing rodents are highly concentrated and predictable over space and time.

INTRODUCTION

Differentiating species according to their relative niche breadth is a common approach in community ecology that can enhance understanding about how species relate to the environment, as well as what roles they play in the ecosystem (Peers et al. 2012). Species with narrow ecological niches are considered specialists, and species with broad ecological niches are considered generalists. Placing a species along the specialist-generalist continuum typically requires quantifying its niche breadth along a particular axis, but this is complicated by variation among resource axes and across spatial and temporal scales (Devictor et al. 2010). Additionally, although specialization is most commonly considered a species attribute, it can be extended to any ecological level such as the individual, population, species, or even community (Bolnick et al. 2003, Devictor et al. 2010). Regardless of how specialization is characterized, a key feature is the selective use of resources from the range of potential resources available (Colwell and Futuyma 1971, Manly et al. 1993).

Local specialization is characterized by consistent use of a particular resource and the absence of a correlation between use and availability of that resource (Kruuk and Parish 1981). Localized patterns of resource use can be influenced by several factors, including competitive interactions among individuals and species, risk of predation (Colwell and Fuentes 1975), and resource distribution or abundance. A population might use a narrow range of resources because they are highly abundant or widely available, or because availability of alternative resources is limited (Lawton et al. 2012). Although a species might have generalized ecologies across its entire range, on a local scale populations may function as specialists (Fox and Marrow 1981, Bolnick et al. 2003).

American badgers (*Taxidea taxus*) are terrestrial carnivores in the family Mustelidae that have been described most often as generalists. Badgers are one of the few carnivores that hunt by scratch-digging (Hildebrand 1985), and they are highly adapted and morphologically specialized to excavate the burrows of tunneling prey (Lampe 1976, Quaife 1978, Minta 1992). Nonetheless, across their geographic range, American badgers prey on a diversity of species in a wide range of habitats. We conducted a comprehensive literature review of habitat use and diet of American badgers to document their functional niche (Appendix A). The literature about badgers indicates that they use a wide variety of habitat types (e.g., sagebrush-steppe, open forests, intermountain valleys, mixed-grass prairies, agricultural fields, roadsides, and mesquite savannah-acacia shrublands) and consume a diversity of food items (e.g., mammals, birds, reptiles, amphibians, fish, insects, arthropods, carrion, eggs, and vegetation). Characterization of habitat use by badgers has ranged from “prairie obligate” (Duquette et al. 2014) to “generalist, non-obligate species” (Paulson 2007). Within the context of diet or food habits, descriptions have ranged from “opportunistic foragers” (Lampe 1982, Sovada et al. 1999) to “strict carnivores” (Messick and Hornocker 1981). The dissimilar characterizations of badgers likely reflects their flexible life history and that patterns of selection are likely influenced by local factors, which vary across the range of the species.

Although badgers appear to exhibit varying degrees of specialization among populations, we hypothesized that badgers would exhibit behaviors more closely aligned with specialists than generalists when food resources are concentrated and highly predictable over space and time. We evaluated resource selection by badgers associated with prairie dog complexes across 3 scales to test the hypothesis that badgers would behave as specialists when foraging on black-tailed prairie dogs (*Cynomys ludovicianus*). At course spatial scales, we predicted that badgers would use prairie dog colonies significantly more than available on the landscape. At an intermediate scale, we predicted that badgers would use prairie dog colonies significantly more than available within their home ranges. At a finer spatial scale, we predicted that within prairie dog colonies, individual badgers would select areas that have high densities of prairie dog burrows. By examining selection across scales, we attempted to evaluate whether specialization of badgers in our study areas was influenced by the scale at which we measured habitat use. Understanding the niche breadth of badgers inhabiting prairie dog ecosystems is especially important because of potential competitive interactions with black-footed ferrets (*Mustela nigripes*), a prairie dog obligate that is federally endangered (U. S. Fish and Wildlife Service 2013) and subject to intraguild predation by badgers (Biggins et al. 1999, 2006a, 2011a).

STUDY AREA

We conducted our field study from 2008 to 2010 on two native prairie grasslands, the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, located approximately 250 km apart in central and southwestern South Dakota, USA, respectively. At the Lower Brule Indian Reservation, our research was conducted on the Fort Hale Bottom prairie dog complex (469857E, 4868645N NAD 83 Zone 14N; hereafter Lower Brule) located in a fragmented mixed-grass prairie dominated by western wheatgrass (*Pascopyrum smithii*), green needlegrass *(Nassella viridula*), buffalograss (*Bouteloua dactyloides*), and needle-and-thread (*Hesperostipa comata*). In 2007, the Lower Brule study site contained 25 prairie dog colonies totaling 642.5 ha (range = 0.1 – 209.1 ha, $\bar{x}$ = 23.8). Previous work using visual count methods (Severson and Plumb 1998) estimated densities of prairie dogs at 44.7/ha and 56.1/ha in 2004 and 2005, respectively (Lower Brule Sioux Tribe *unpublished data*). The area is primarily used for livestock grazing but cultivated agriculture also is common.

Our research at the Buffalo Gap National Grasslands occurred on the Heck Table prairie dog complex (699205E, 4843996N NAD 83 Zone 13N; hereafter Buffalo Gap). The site is a mixed-grass prairie dominated by western wheatgrass, buffalograss, blue grama (*Bouteloua gracilis*), and prickly pear cactus (*Opuntia polyacantha*), and it is nearly devoid of tree and shrub species (Schroeder 2007, Livieri and Anderson 2012). In 2007, the Buffalo Gap study site supported 31 colonies of prairie dogs that totaled 1192.9 ha (range = 0.2 – 284.6 ha, $\bar{x}$ = 38.5 ha). Densities of prairie dogs were estimated at 27.9/ha in this area in 1999 (Biggins et al. 2011b) and 41.0/ha on nearby colonies in the Conata Basin in 2007 (Eads et al. 2011) using counts of active burrows as indices (Biggins et al. 1993). Primary land uses for the area are cattle grazing and recreation (Livieri and Anderson 2012).

METHODS

Badger capture and monitoring. –We searched prairie dog colonies to locate badgers for capture. We set padded leg-hold traps (#3 coil spring, Victor Soft Catch, Woodstream Corp., Lititz, Pennsylvania, USA) at the entrance of occupied badger burrows. Trapped individuals were chemically immobilized with an intramuscular injection of ketamine hydrochloride and xylazine hydrochloride (15 mg/kg body weight and 1.5mg/kg, respectively; Goodrich and Buskirk 1998), marked with a passive integrated transponder, and fitted with a harness-style radio-transmitter weighing approximately 100-110g (Advanced Telemetry Systems, Isanti, Minnesota, USA). The anesthetic effects of xylazine hydrochloride were reversed by intravenous injection of yohimbine (0.125 mg/kg; Goodrich and Buskirk 1998). Relocations of telemetered badgers were primarily obtained at night.

We monitored badgers year-round at Lower Brule and seasonally at Buffalo Gap. Monitoring occurred during November 2008 – November 2010 at Lower Brule, and August – November 2008 and May – November 2009 at Buffalo Gap. We considered juvenile badgers independent of their parents on 1-September of the year of their birth and did not include locations of juveniles prior to this date in our analyses. Juveniles were considered adults on 1-April of the year after their birth. We did not include locations of badgers collected during periods of extended inactivity associated with cold temperatures to minimize serial autocorrelation (Minta 1992, 1993).

Prairie dog colony and burrow mapping. –We mapped prairie dog colonies at Lower Brule in August 2007, and personnel of the U. S. Forest Service mapped colonies at Buffalo Gap during May – September 2007 using Trimble® GeoXM™ GPS receivers (1-m accuracy) while driving an ATV or walking along the perimeters of the colonies. Edges of colonies were distinguished by the distinct difference in vegetation height caused by foraging and vegetation clipping behavior of black-tailed prairie dogs (Koford 1958, Hoogland 1995). We imported data into ArcGIS (v. 9.3, ESRI, Redlands, California, USA) to delineate resource availability and to conduct course-scale spatial analyses.

Burrow openings were mapped using Trimble® GeoXM™ GPS receivers on a subset of colonies at the Lower Brule site during July – August 2010. Burrow openings were categorized as active or inactive, based on presence of a prairie dog, fresh scat, fresh digging, and spider webs (*sensu* Biggins et al. 1993).

For our fine-scale analysis, we buffered all openings to prairie dog burrows by 20-m-radius circular polygons and dissolved internal boundaries to create a single outer boundary for prairie dog colonies using ArcGIS (*sensu* Biggins et al. 2006b). This fine-scaled approach differs from the intermediate- and course-scale approaches because the colony boundary more accurately reflects the distribution of burrow openings available to prairie dogs and excludes spaces within the outer boundary that are > 40 m from the nearest burrow.

Spatial and statistical analyses. –We evaluated selection for prairie dogs at the scales of prairie dog colonies, badger home ranges, and also within the colonies using a use-availability framework (Johnson 1980, Manly et al. 2002). We determined habitat "available" for badgers for the coarse-scale analysis by creating a minimum convex polygon from all badger locations at each study site using ArcGIS. Badgers were marked in 2 disjunct areas at the Lower Brule study site; therefore, a minimum convex polygon was created for each area, and available habitat was determined by combining the total area of both polygons. To evaluate selection at the coarse scale, we compared the proportion of badger locations recorded "on" prairie dog colonies to "off" prairie dog colonies using binomial proportion Z-tests. We also tested whether similar results were apparent between the sexes and age categories (adults versus juveniles) using Chi-square tests. When appropriate, our analyses were one-tailed or one-sided tests because our tests reflected our hypotheses that badgers would select for prairie dog colonies at course scales and areas within prairie dog colonies that have high densities of burrows at fine scales.

For our intermediate-scale analysis, we evaluated selection for prairie dog colonies by badgers within their home ranges. We generated utilization distributions (UDs) for each badger for which we recorded $\geq$27 locations to estimate the relative intensity of use across space (Van Winkle 1975, Kernohan et al. 2001). We used fixed-kernel estimation (Worton 1989) with a likelihood cross-validation smoothing parameter to estimate individual 95% UDs with a grid cell size of 30 x 30 m using the Hawth's Tools extension (Beyer 2004) in ArcGIS and Animal Space Use (v. 1.3, Horne and Garton 2009). For each badger, we evaluated resource use within the home range by comparing the proportion of the volume of the UD that overlapped prairie dog colonies with the proportion of the area of the UD that overlapped colonies using a paired *Z*-test. Area and UD volume were calculated using zonal statistics, spatial analyst, and Hawth's Tools (Beyer 2004) in ArcGIS.

Our fine-scale analysis evaluated selection by badgers for areas within prairie dog colonies with high densities of prairie dogs by evaluating the association between badger locations and prairie dog burrows. We conducted this analysis on a sub-set of prairie dog colonies at the Lower Brule study site where we mapped prairie dog burrows. We compared the number of burrows within 20-m radius circular plots (0.13 ha) centered on badger telemetry locations and on random locations (*sensu* Biggins et al. 2006b) that were cast within the same prairie dog colony, but outside of the circular plots representing badger use areas. We compared the total number of prairie dog burrows in used and random plots using a general linear mixed model with a repeated measure on individual badgers using Proc Mixed in SAS (v. 9.3, SAS Institute Inc., Cary, North Carolina, USA). Colony and location (used or random) were treated as fixed effects.

RESULTS

Prairie dog colonies comprised relatively small portions of our study sites. The Lower Brule site was comprised of 522.2 ha of prairie dog colonies and 2,438.1 ha of non-colony habitat. The Buffalo Gap site included 2,401.3 ha of prairie dog colonies and 9,455.4 ha of non-colony habitat. Combined, prairie dog colonies comprised 20% of the available habitat. During our study, we recorded 852 locations from 22 badgers: 7 adult females, 8 adult males, 2 juvenile males, and 5 badgers (3 females, 2 males) that were radio-tracked as juveniles and as adults ($\bar{x}$ = 38.7 locations per individual, range = 4 – 99, SD = 25.3). At Lower Brule, radio-marked badgers (n = 10) used 11 colonies that averaged 30.9 ha in size (range = 0.8 – 207.7 ha, SD = 62.1 ha). At Buffalo Gap, marked badgers (n = 12) used 8 colonies that averaged 99.6 ha in size (range = 1.8 – 284.6 ha, SD = 120.1 ha). Densities of prairie dog burrows averaged 337.4/ha (range = 259.1 – 439.2/ha, SD = 90.6 ha) on 5 prairie dog colonies at Lower Brule (Table 3-1).

Badgers in our study selected for prairie dog colonies at the broadest spatial scale we examined. There was no difference in the relative use of prairie dog colonies by badgers between study sites (Lower Brule = 66.5% and Buffalo Gap = 67.7%; χ^2 = 0.131, P = 0.718), so data from both sites were combined for this component of our analyses. Badgers (n = 22) used prairie dog colonies an average of 66.9% (range = 0 – 100%, SE = 1.6%), which was significantly more than predicted based on the proportion of prairie dog colony habitat (20%) within the available habitat (Z = 34.23, $P < 0.001$). Although the proportion of locations on prairie dog colonies was significantly greater for female badgers (70.3%, SE = 2.1%) than males (62.9%, SE = 2.4%, χ^2 = 5.18, P = 0.023), selection for prairie dog colonies was evident for both sexes (female: Z = 26.99, $P < 0.0001$; males: Z = 21.22, P <

0.001; Figure 3-1A). Similarly, the proportion of locations on prairie dog colonies was significantly greater for adult badgers (70.6%, SE = 1.8%) as compared to juveniles (57.3%, SE = 3.2%; $\chi^2 = 13.77$, $P < 0.001$), but both age categories exhibited significant selection for prairie dog colonies (adults: $Z = 31.34$, $P < 0.001$; juveniles: $Z = 14.42$, $P < 0.001$; Figure 3-1B).

Badgers also selected for prairie dog colonies at intermediate scales. We generated UDs for 15 badgers: 6 adult females, 1 juvenile female, 4 adult males, 3 juvenile males, and 1 female that was radio-tracked as a juvenile and as an adult (separate UDs were created for each age class), for which 726 locations were recorded ($\bar{x} = 45.4$, range = 27 – 92, SD = 20.7). The proportion of the volume of 95% UDs within prairie dog colonies averaged 51.7% (range = 23.5 – 73.9%, SE = 4.2%), which was significantly greater than the proportion of area of badger UDs within prairie dog colonies ($\bar{x} =$ 37.8%, range = 11.8 – 63.4%, SE = 4.2%; $Z = 6.09$, P < 0.001; Figure 3-2). These results indicate that within home ranges, badgers used prairie dog habitat more than expected based on the amount of the home range that overlapped with prairie dog colonies.

At fine scales within prairie dog colonies, badgers (n = 8) selected for areas with high densities of prairie dog burrows. The mean number of burrows within plots around badger locations was 44.2 (n = 196, range = 3 – 99, SE = 1.22) compared to an average of 39.6 within random plots (n = 196, range = 0 – 101, SE = 1.43). Locations of badgers were associated with higher densities of burrows than random plots ($F_{1,\,382} = 5.80$, $P = 0.017$; Figure 3-3). This pattern was relatively consistent across colonies (location x colony interaction; $F_{1,\,382} = 1.86$, $P = 0.117$) suggesting that selection for prairie dogs was not a function of a particular arrangement or density of burrows on different colonies.

DISCUSSION

In our study area, badgers selectively used prairie dog colonies on the landscape and within their home ranges, and by focused use within colonies on areas with relatively high densities of prairie dogs. Although American badgers have a broad functional niche across their geographic range, in our study, they exhibited strong selection for a relatively narrow range of habitat resources. The strong selection for prairie dogs by badgers at multiple scales represents a behavioral pattern that is more characteristic of a specialist than a generalist.

At a landscape scale, all sex and age categories of badgers selected for colonies of black-tailed prairie dogs. A similar pattern was reported for adult female badgers but not adult males inhabiting areas with complexes of white-tailed prairie dogs (*C. leucurus*; Goodrich and Buskirk 1998).

The difference in selection by male badgers between the two studies might be explained by differences between the species of prairie dog and intersexual differences in the spatial organization of badgers. Colonies of white-tailed prairie dogs are less densely populated, lack distinctive boundaries, and are more patchily distributed on the landscape than colonies of black-tailed prairie dogs (Tileston and Lechleitner 1966, Menkens et al. 1987, Hoogland 1995); thus providing a more distributed food source than black-tailed prairie dogs. Additionally, male and female badgers have different space use patterns. The spatial organization of female badgers is shaped largely by the distribution of food resources while male spatial patterns are determined primarily by the distribution of females (Messick and Hornocker 1981, Minta 1993, Goodrich and Buskirk 1998). In landscapes with densely populated colonies of black-tailed prairie dogs, such as our study sites, prey is not only predictable but also highly concentrated, and in our study, both male and female badgers exhibited strong selection at a coarse scale for prairie dog habitat.

Badgers in our study also selectively used prairie dog colonies within their home ranges. Goodrich and Buskirk (1998) documented several female badgers with home ranges completely within colonies of white-tailed prairie dogs. Although the size of the colonies in our study likely precluded a similar pattern, prairie dog colonies were the obvious focal area for nearly all the badgers in our study. The abundance of prey drives patterns of habitat selection for many predators including least weasels (*M. nivalis*; Erlinge 1974, Klemola et al. 1999), a specialist of voles (*Microtus* spp.; King and Moors 1979) and lynx (*Lynx canadensis*, Murray et al. 1994), a specialist of snowshoe hares (*Lepus americanus*; O'Donoghue et al. 1998). The unequal use of their home range and the disproportionate use of prairie dog colonies suggest that for badgers, the selection of prairie dog colonies as habitat is due to the availability of abundant burrowing prey.

Within prairie dog colonies used by badgers, individuals selected for areas that had high densities of prairie dog burrows and presumably abundant prey. Our results are consistent with those of Eads et al. (2013) who reported that badgers selected for areas within prairie dog colonies that had high densities of active burrows. In addition to prey availability, a reduction in energetic costs of burrow construction when excavating existing prairie dog burrows also might influence badgers to select prairie dog burrows when burrows are created for shelter. Shearing hardened soils and pushing loosened soil is energetically costly for subterranean organisms such as the Botta's pocket gopher (*Thomomys bottae*; Vleck 1979) and degu (*Octodon degus*; (Ebensperger and Bozinovic 2000). The excavation of existing burrows by badgers requires a smaller volume of soil to be loosened and pushed to the surface as compared to undisturbed ground. Although reduced energetic costs associated with burrow construction might influence selection patterns, we believe badgers most likely selected for areas of prairie dog colonies that had high densities of burrows because of the abundance of prey.

Our fine-scale analysis was focused on a subset of colonies at the Lower Brule site where we had mapped all burrows, and consequently, a subset of radio-marked badgers, which precluded a comparison of patterns between sex and age classes. Given differences in space use between the sexes (Messick and Hornocker 1981, Minta 1993, Goodrich and Buskirk 1998) and potential dominance relationships between adults and independent juveniles (Sandell 1989, Minta 1992, Minta 1993), we predict that fine-scale resource selection also differs among these categories; however, studies with larger samples of individually marked badgers are needed to test this prediction.

The strong selection for prairie dog colonies by badgers in our study contrasts the association between prairie dog colonies and the swift fox (*Vulpes velox*), a prairie carnivore that is considered a dietary generalist (Sovada et al. 2001, Harrison 2003). Swift foxes often are associated with prairie dog ecosystems (Sharps and Uresk 1990, Lomolino and Smith 2003), but Nicholson et al. (2006) reported that swift foxes used prairie dog colonies less than expected, and Sasmal et al. (2011) reported that female foxes used prairie dog colonies in proportion to their availability. If the use of prairie dog colonies by swift foxes is typical of generalist carnivores, we would expect similar selection patterns by badgers. The contrasting use of prairie dog colonies between swift foxes and badgers, 2 species that are often characterized as generalists, lends support to our characterization that badgers behaved as prairie dog specialists during our study.

The results of our fine-scale analysis of badger use of prairie dog colonies are similar to selection patterns of black-footed ferrets, a prairie dog specialist. Ferrets also select for areas within prairie dog colonies with high densities of prairie dog burrows (Biggins et al. 2006b, Eads et al. 2011, Jachowski et al. 2011). Ferrets are considered prairie dog specialists because they prey primarily on prairie dogs, use prairie dog burrows as protective cover, and do not use habitats other than prairie dog colonies (Sheets et al. 1972, Campbell et al. 1987, Biggins et al. 2006b). Early research suggested that prairie dogs comprised approximately 90% of the diet of ferrets (Sheets et al. 1972, Campbell et al. 1987). However, recent analyses using stable isotopes indicated prairie dogs comprised 61 – 76% of the diet of ferrets (Brickner et al. 2014), which suggests ferrets consume a broader range of prey items than previously thought. Although our study did not include an analysis of diet, Goodrich and Buskirk (1998) reported that prairie dogs were present in 50 – 57% of the samples from badgers. We suggest that similarity in fine-scale patterns of habitat selection and diet of ferrets and badgers also supports the contention that badgers in our study exhibited local specialization on prairie dogs.

Local specialization on prairie dogs by badgers would seem to have ecological consequences for endangered black-footed ferrets, including intraguild predation. Coexistence between the species could be facilitated by avoidance of badgers by ferrets. Indeed, at our study sites, adult female badgers were avoided by ferrets, especially adult female ferrets (Chapter 1). In the absence of avoidance strategies, coexistence of ferrets and badgers at fine spatial scales would likely be facilitated, in part, by the relatively high efficiency of ferrets to prey on prairie dogs as compared to badgers (i.e., exploitative competition) and by the selection of burrow systems with multiple openings, which likely lowers the risk of predation by badgers (Biggins 2012). Although ferrets are sometimes killed by badgers (Biggins et al. 1999, 2006a, 2011a), mechanisms appear to exist that facilitate the co-occurrence of these 2 prairie dog specialists.

Among carnivores, prey profitability or predictability is known to influence local resource use (Martin et al. 1995, Panzacchi et al. 2008). For badgers, the propensity to act as generalists or specialists across their geographic range appears to be influenced by available prey. For example, Sargeant and Warner (1972) reported that use of grasslands and dense woodlots by badgers in Minnesota was associated with high densities of plains pocket gophers (*Geomys bursarius*). Similarly, the abundance and distribution of badgers was related to concentrations of Belding's ground squirrels (*Urocitellus beldingi*) in an agriculturally developed, semi-arid area of southern Idaho (Todd 1980). In British Columbia, badgers used agricultural lands, grasslands, and open forests, which were associated with the distribution of Columbian ground squirrels (*U. columbianus*; Newhouse and Kinley 2000, Kinley et al. 2014). Indeed, the selection of habitats by badgers across their range often appears to be a function of specialized use of a diverse suite of burrowing rodents across habitats. Our results and the research of others (e.g., Goodrich and Buskirk 1998, Eads et al. 2013) suggests that badgers are more likely to behave as specialists when burrowing rodents are highly concentrated and predictable over space and time. Badgers that inhabit landscapes without predictable and abundant burrowing prey likely behave more like generalists and opportunistically use a variety of habitats in search of diverse prey (e.g., Warner and ver Steeg 1995, Sovada et al. 1999, Duquette et al. 2014).

Local specialization by generalists has been reported in other taxa. For example, European badgers (*Meles meles*) sometimes specialize on earthworms (*Lumbricus* spp., Kruuk and Parish 1981), olive fruits (*Olea europea*, Kruuk and de Kock 1981) or young rabbits (*Orxctolagus cuniculus*, Martin et al. 1995, but see Revilla and Palomares 2002). Red foxes (*Vulpes vulpes*) behave as specialists when inhabiting fragmented landscapes with high prey densities (Panzacchi et al. 2008). For badgers, colonial ground squirrels provide concentrated food sources that are predictable over space and time, and black-tailed prairie dogs are among the largest of colonial ground squirrels and create the most spatially concentrated colonies (Hoogland 1995).

The position of American badgers on the generalist-specialist continuum is likely a function of prey densities and scale. Badgers might be more appropriately categorized as specialists at local scales where prey concentration is high, but generalists at broader geographic scales. Furthermore, placing a species along the specialist-generalist continuum is typically within the context of a particular axis (Devictor et al. 2010). Because prairie dogs create distinctive patches of unique habitat, the dietary and habitat axes of prairie dogs are intertwined. In our study, badgers could be characterized as habitat specialists because of the strong selection for prairie dog colonies. Similarly, badgers also could be considered dietary specialists because prairie dogs comprise a high proportion of the diet of badgers (Goodrich and Buskirk 1998) and badgers in our study and others (Eads et al. 2013) selected for areas of prairie dog colonies with high densities of prairie dog burrows and abundant prey. We suggest that badgers that exhibit local specialization of prairie dogs could aptly be characterized as “facultative resource specialists” because badgers act as specialists on prairie dogs along both habitat and dietary axes.

Our results provide evidence of local specialization by badgers. Badgers selected for prairie dog colonies and selected for areas of prairie dog colonies that had high densities of prairie dog burrows, where prey is abundant. On multiple scales, badgers in our study exhibited a narrow use of resources in comparison to the resources available. Badgers in our study displayed patterns of selection similar to black-footed ferrets, a specialist, and in contrast to those of swift foxes, a generalist. Our results suggest that local specialization is more likely to occur in landscapes where burrowing rodents are highly concentrated and predictable over space and time. Badgers that inhabit landscapes without predictable and abundant burrowing prey likely behave more like generalists and use a variety of habitats in search of diverse prey.

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Table 3-1. Characteristics of a subset of prairie dog colonies used by badgers on the Lower Brule Indian Reservation, SD, 2010.

Colony	Size (ha)	Total burrows/ha (n)	Active burrows/ha (n)
Cattle Guard	8.6	439.2 (3797)	259.6 (2244)
Sheldon South	7.3	432.4 (3138)	300.6 (2181)
Sheldon East	2.9	290.3 (854)	78.2 (230)
High Otter	11.6	265.8 (3079)	141.4 (1638)
Badger Head	12.8	259.1 (3321)	169.3 (2170)

Figure 3-1. Proportion of badger locations (n = 852) recorded on prairie dog colonies by sex (A) and age (B) categories from badgers radio-marked (n = 22) on the Lower Brule Indian Reservation, SD, and Buffalo Gap National Grasslands, SD, 2008 – 2010. Horizontal line represents the proportion of prairie dog colonies within the study sites.

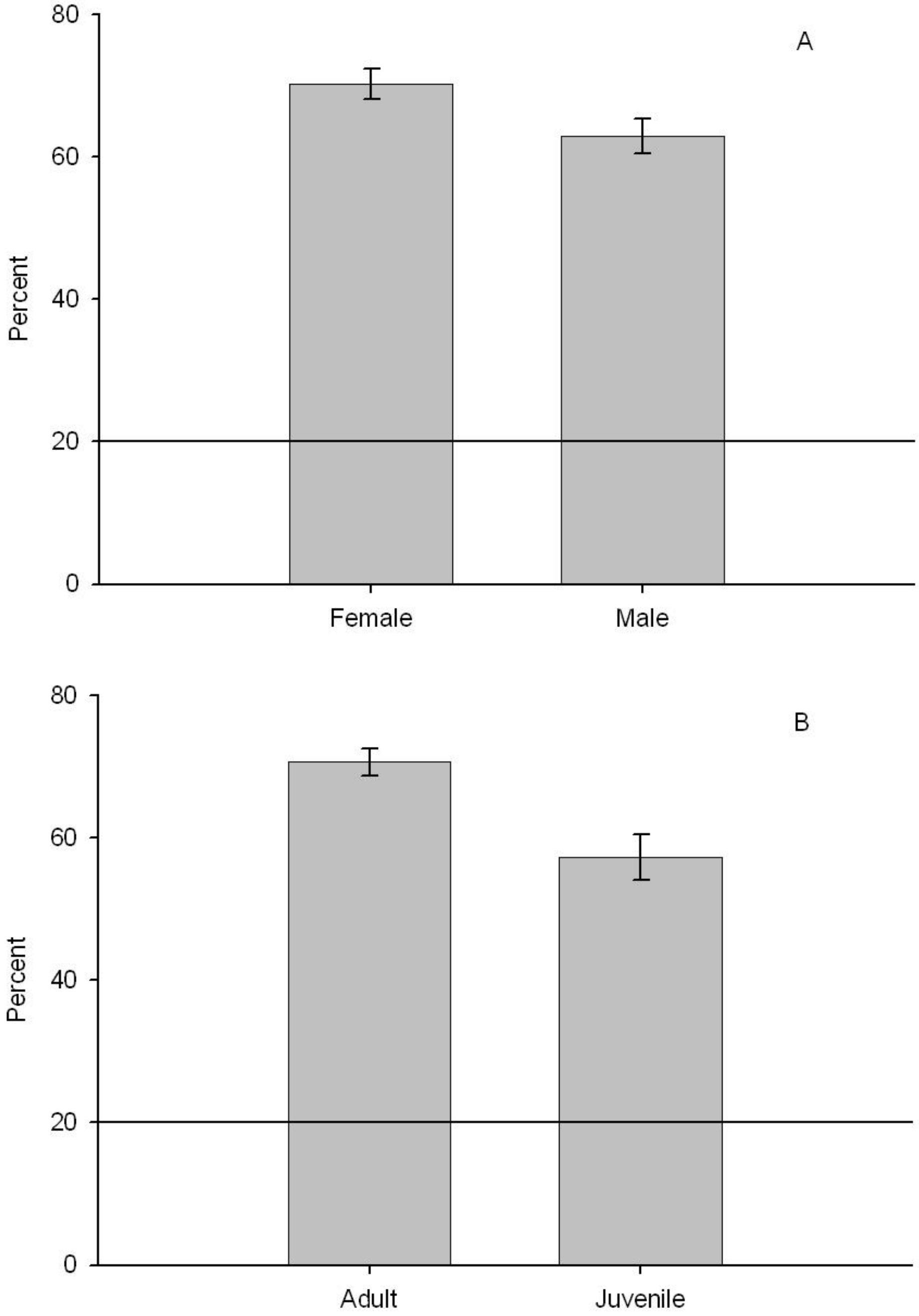


Figure 3-2. Average percent of volume and area of badger utilization distributions (UDs; n = 15) within prairie dog colonies on the Lower Brule Indian Reservation, SD, and Buffalo Gap National Grasslands, SD, 2008 – 2010.

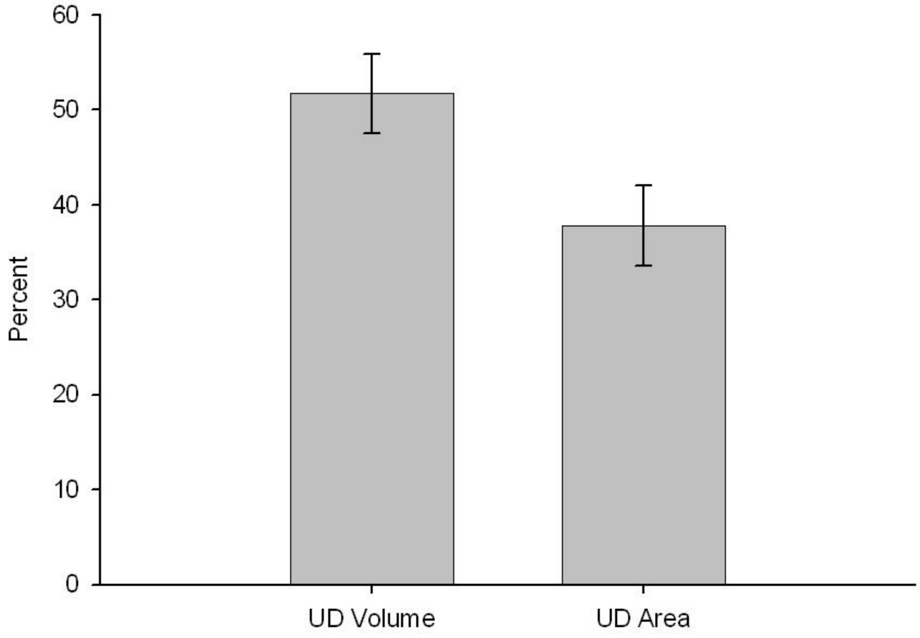
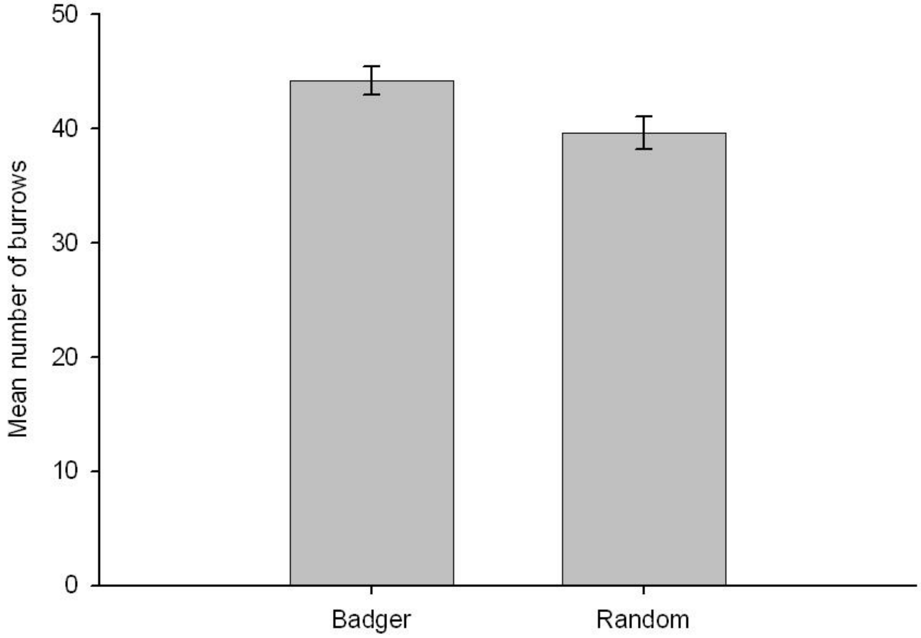


Figure 3-3. Mean number of black-tailed prairie dog burrows within 0.13-ha circular plots centered on badger (n = 196) and random (n = 196) locations on the Lower Brule Indian Reservation, SD, 2008 – 2010.



DISSERTATION CONCLUSION

The conservation of communities and ecosystems requires knowledge about how the behavior of a species might be influenced by the presence of others and how environmental factors can affect population dynamics. This dissertation examined some aspects of the ecological relationships among black-footed ferrets (*Mustela nigripes*), American badgers (*Taxidea taxus*), and black-tailed prairie dogs (*Cynomys ludovicianus*) with the goal of deepening our understanding of the ecology of all 3 species so that conservation and management of grassland ecosystems can be improved.

We documented asymmetric patterns of avoidance of badgers by ferrets based on the sex of both species. Female ferrets avoided adult female badgers, but not male badgers, and male ferrets exhibited less avoidance than female ferrets. Additionally, avoidance decreased with increasing densities of prairie dogs. Our results suggest that intersexual differences in space use by badgers creates varying distributions of predation risk that are perceived by the smaller carnivore (ferrets), and that females respond more sensitively than males to that risk. Our results also support a conclusion by Biggins et al. (2006) that the positive association between security and food resources likely reduces the need for ferrets to trade off productive but risky habitats for less productive, safer ones.

We showed that reproduction by prairie dogs was strongly influenced by precipitation received during the previous year and winter severity. Harsh winter conditions resulted in a marked decline in reproduction during one of the years of our study. Furthermore, we showed that reproduction by ferrets varied little across years of our study, despite a marked decrease in the reproduction of prairie dogs during one year. Regional conservation strategies are increasingly including provisions for system responses to changing climate patterns (e.g., Browne and Humburg 2010, Schrag 2011), and our results suggest that these considerations should be incorporated into conservation planning for the prairie dog – ferret system.

Lastly, we provide evidence of local specialization by badgers. Badgers selected for prairie dog colonies and selected for areas within prairie dog colonies that had high densities of prairie dog burrows. On multiple scales, badgers in our study exhibited a narrow use of resources in comparison to the resources available. Badgers in our study displayed patterns of selection similar to black-footed ferrets, a specialist, and contrasted those of swift fox, a generalist. Our results suggest that local specialization is more likely to occur in landscapes where burrowing rodents are highly concentrated and predictable over space and time. Badgers that inhabit landscapes without predictable and abundant burrowing prey likely behave more like generalists and use a variety of habitats in search of diverse prey.

The common thread of our study was the influence of prairie dogs on the ecology of 2 native carnivores. Without adequate conservation, the functional role of prairie dogs in the grassland ecosystem as a keystone species will be diminished; thus the conservation of prairie dog colonies will not only benefit prairie dogs, but also badgers, ferrets, and other species associated with the prairie dog – grassland ecosystem.

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APPENDIX A. LITERATURE REVIEW OF DIET AND HABITAT USE BY AMERICAN BADGERS (*TAXIDEA TAXUS*).

Citation	Location	Habitat association	Food Items
Apps et al. 2002	British Columbia	Positive relationship with non-forest or open-canopied forest, open range and agriculture, highways and linear disturbances.	Not studied but Columbian ground squirrels (*Urocitellus columbianus*) and northern pocket gophers (*Thomomys talpoides*) are potential burrowing prey.
Armitage 2004	Colorado	Not studied. Study area: Intermountain valley. Badgers sometimes use marmot colonies.	Badgers killed 67 of 1423 yellow-belied marmots (*Marmota flaviventris)*; predation risk was highest for young, intermediate for yearlings, and low for adult marmots. Author states predation on marmots by badgers is underestimated.
Azevedo et al. 2006	Saskatchewan	Not studied. Study area: cultivated agriculture, grasslands, and wetlands.	Primarily mammalian prey, birds and eggshells, insects, amphibians also present. Authors state badgers have a generalized diet, broad dietary breadth. No inter-annual variation in total diet or seasonal changes for mammalian component.
Bylo et al. 2014	Saskatchewan	Within upland habitats, increased grazing intensity in experimental plots increased indices for ground squirrel and badger use. Study area: grasslands.	Not studied directly but badgers likely selected habitat because of the presence of 13-lined and Richardson's ground squirrels (*Ictidomus tridecemlineatus and Urocitellus richardsonii*).
Collins et al. 2007	Texas	Not studied. Study area: grassland/savanna [mesquite (*Prosopis glandulosa*) – granjeno (*Celtis pallida*)].	Prickly pear fruit, mesquite bean pods, and rodents.

Collins et al. 2012	Texas	Badgers preferred mesquite savannah and acacia (*Acacia* spp.) shrublands. Burrows associated with mesquite and bufflegrass (*Pennistum ciliare*).	Not studied.
Duquette 2008 (Thesis)	Ohio, Indiana	Study area: highly fragmented matrix of agriculture. Habitat selection reported in Duquette et al. 2014.	Primarily (54%) consumed *Peromyscus* spp. and other rodents, but also eastern cottontail rabbits (*Sylvilagus floridanus*), and woodchuck (*Marmota monax*). No non-mammalian prey.
Duquette et al. 2014	Ohio, Indiana	Badgers selected for croplands, upland forests, pastures.	Not studied.
Eads et al. 2013	South Dakota	Badgers select for areas within black-tailed prairie dog (*Cynomys ludovicianus*) colonies with high burrow densities. Study area: prairie dog colonies in mixed-grass prairie.	Not studied but high burrow density areas are associated with abundant prey (prairie dogs).
Errington 1937	Iowa	Not studied. Study area: tall-grass prairie reserve.	Primarily (53%) consumed 13-lined and Franklin's ground squirrels (*Poliocitellus franklinii*), and (30%) *Microtus* spp. and *Peromyscus* spp., but also insects, birds, bird and reptile eggshells, frogs, and fish.
Goodrich and Buskirk 1998	Wyoming	Study area: shrub-steppe. Females used prairie dog colonies more than expected but males did not. Some females were located only on prairie dog colonies.	Percent of samples containing item: 52% white-tailed prairie dog (*Cynomys leucurus*), 29% *Urocitellus* ground squirrels, 20% Audubon's cottontail rabbits (*Sylvilagus audubonii*), and 2-9% of *Microtus spp.*, deer mice (*Peromyscus maniculatus*), and white-tailed jackrabbits (*Lepus townsendii*).

Hoodicoff 2003 (Thesis)	British Columbia	Badger burrows located in cultivated fields, pastures, power-line rights-of-ways, natural grasslands, and roadsides. Study area: intermountain valleys with grassland-sagebrush (*Artemesia tridentata*) at lower elevations, and ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) at mid-elevations.	Badger burrows associated with sign of burrowing prey. Badgers had access to northern pocket gophers, Columbian ground squirrels, other small rodents, and yellow-bellied marmots.
Huck 2010 (Thesis)	California	Study area: Grasslands and open woodlands. Reproductive den sites differed from other sites by the extent of ground vegetation, prey density, presence of other predators, and slope.	Not studied.
Jense 1968 (Thesis)	South Dakota	Not studied. Study area: Cultivated agriculture, haylands, and mixed-grass prairie pastures.	Deer mice, 13-lined ground squirrels, meadow voles (*Microtus pennsylvanicus*), white-tailed jackrabbits, and eastern cottontail rabbits were most common prey items. Birds, eggs, toads (*Anaxyrus cognatus*), grains, beetles, and bees were consumed when available.
Kinley et al. 2014	British Columbia	Badgers selected for cultivated agriculture lands, grasslands, open forest, and light soils, all of which were associated with Columbian ground squirrels.	Not studied.
Lampe 1982	Minnesota	Not studied. Study area: tallgrass prairie, cultivated agriculture, with deciduous and mixed coniferous uplands.	Plains pocket gophers (*Geomys bursarius*) were the most frequent prey item. Badgers also consumed *Peromyscus* spp., southern red-backed voles (*Clethrionomys gapperi*), eastern

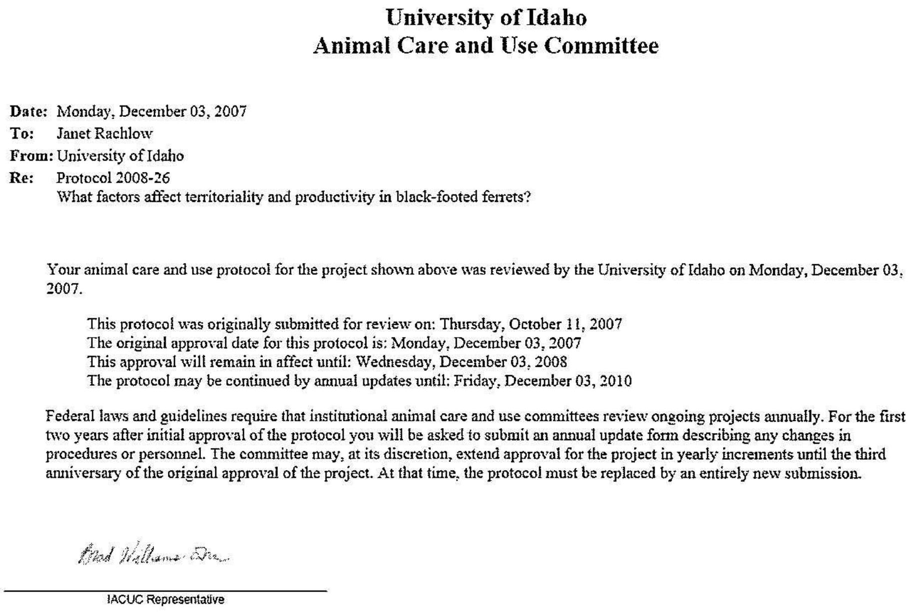
			chipmunks (*Tamias striatus*), *Microtus* spp., woodchucks, 13-lined and Franklin’s ground squirrels, muskrats (*Ondatra zibethicus*), eastern cottontails, birds, insects, and reptiles.
Lindzey 1971	Idaho, Utah	Not studied. Study area: sagebrush-steppe.	Microtine and Cricetine rodents were the most frequent prey items. Lagomorphs [black-tailed jackrabbits (*Lepus californicus*), Nuttall’s cottontail rabbits (*Sylvilagus nuttallii*) and pygmy rabbits (*Brachylagus idahoensis*)] were common prey items. Also consumed other species of small rodents, birds, insects, reptiles, and carrion. Seasonal variability in prey items.
Messick and Hornocker 1981	Idaho	Not studied. Study area: sagebrush-steppe.	Townsend’s ground squirrels (*Urocitellus townsendii*) most frequent (70% of samples). Lagomorphs, deer mice, kangaroo rats (*Dipodomys* spp.), other small rodents, reptiles, arthrodpods, birds, eggs, vegetation, and carrion also consumed. Townsend’s ground squirrels populations declined markedly but decreased only slightly in badger diet but badgers did increase consumption of other prey items during same time period.
Minta 1993	Wyoming	Not studied. Study area: sagebrush-grasslands.	Uinta ground squirrels (*Urocitellus armatus*) >75% of diet.

Newhouse and Kinley 2000	British Columbia	Badgers selected for non-forested land but used forested lands with crown closure up to 85%. Badgers occurred closer to roads than expected. Burrows were located near Columbian ground squirrels more than their availability.	Diet included Columbian ground squirrels, red-backed voles (*Clethrionomys gapperi*), beetles, Passerines, common loons (*Gavia immer*), and fish.
Packham and Hoodicoff 2004	British Columbia	Not studied but 23% of badger burrows and sightings were within 50 m and 12% were within 15 m of a wetland or lake. Study area: inter-mountain valley.	Prey remains at burrow entrances: rabbits, marmot, muskrat, Columbian ground squirrels, red squirrels (*Tamiascirus hudsonicus*), murids, birds, amphibians and fish. Scavenged on mule deer (*Odocoileus hemionus*).
Paulson 2007 (Thesis)	Washington	At a course scale, badgers did not select burrow sites based on any habitat variables evaluated. At a fine scale, badgers selected burrow sites based on availability of prey and cover (that might have been selected by prey). Author states badgers are non-obligate, habitat generalists. Study area: shrub-steppe and cultivated agriculture.	Northern pocket gopher was the most likely prey available.
Proulx and MacKenzie 2012	Saskatchewan	Not studied. Study area: 69% land was cultivated, numerous roads.	Not studied.
Quinn 2008 (Dissertation)	California	At a course scale, badgers selected for grasslands, scrub, and oak (*Quercus* spp.) woodlands, and areas close to recreational trails. At a fine scale, badgers selected for intermediate slopes, native grassland and scrub habitat, and within 500 m of trails.	Not studied but common prey available were Botta's pocket gophers (*Thomomys bottae*), California voles (*Microtus californicus*), kangaroo rats, and dusky-footed woodrats (*Neotoma fuscipes*).

Sargeant and Warner 1972	Minnesota	Badger used idle grass fields and dense stands of oak and hazel (*Corylus americana*). Badgers used areas with high concentration of plains pocket gopher mounds.	Not an extensive analysis. A few scat contained plains pocket gophers and insects.
Snead and Hendrickson 1942	Iowa	Not studied. Study area: gently rolling prairie, pastures, hayfields, numerous wetlands and streams.	Common diet items included 13-lined and Franklin's ground squirrels, *Peromyscus* spp., and *Microtus* spp. Other items include Mearns cottontails (*Sylvilagus floridanus mearnsi*), insects, birds, plains pocket gophers, reptiles, and vegetation. Seasonal variation in food items.
Sovada et al. 1999	Minnesota, North Dakota	Not studied. Study area: intensive cultivated agriculture, haylands, pastures, wildlife management areas, and lands enrolled in the Conservation Reserve Program. Numerous wetlands.	Mammals in 96% of samples. Mice (Muridae, Heteromyidae, Zapodidae) most prevalent, then pocket gophers (Geomyidae) and ground squirrels (Sciuridae); also white-tailed jackrabbit, birds (ducklings, eggs), insects, reptiles, amphibians, snails, and plant material. No seasonal effect for mammal frequency in diet. Insects second in frequency but low volume. Birds more common in summer than spring.
Todd 1980 (Thesis)	Idaho	Areas with intensive agriculture and annual vegetation supported greater number of badgers and ground squirrels than native vegetation. Study site: agriculturally developed, semi-arid desert.	Not studied but badger abundance and distribution was associated with concentrations of Belding's ground squirrels (*Urocitellus beldingi*).

van Vuren 2001	Colorado	Not studied. Study area: Intermountain valley, 2850-2930 m in elevation.	Badgers preyed on yellow-bellied marmots.
Warner and Ver Steeg 1995	Illinois	Badgers preferentially used "Undisturbed" cover types (hedgerows, roadsides, alfalfa fields, CRP fields) over "disturbed" (agriculture) cover types.	Majority (89%) of samples mammalian prey: *Peromyscus* spp., *Microtus* spp., plains pocket gopher, 13-lined and *Urocitellus* ground squirrels, meadow jumping mouse (*Zapus hudsonius*), and woodchucks. Badgers also consumed snakes, toads, birds, insects, and plant material.

APPENDIX B: ANIMAL CARE AND USE PERMIT



University of Idaho
Animal Care and Use Committee

Date: Monday, December 03, 2007
To: Janet Rachlow
From: University of Idaho
Re: Protocol 2008-26
What factors affect territoriality and productivity in black-footed ferrets?

Your animal care and use protocol for the project shown above was reviewed by the University of Idaho on Monday, December 03, 2007.

This protocol was originally submitted for review on: Thursday, October 11, 2007
The original approval date for this protocol is: Monday, December 03, 2007
This approval will remain in affect until: Wednesday, December 03, 2008
The protocol may be continued by annual updates until: Friday, December 03, 2010

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.

Brad Williams

IACUC Representative