

When generalists behave as specialists: local specialization by American badgers (*Taxidea taxus*)

S.M. Grassel and J.L. Rachlow

Abstract: 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. Although a species might exhibit a generalized ecology across its entire range, on a local scale, individuals might function as specialists. American badgers (*Taxidea taxus* (Schreber, 1777)) are terrestrial carnivores that have been described most often as generalists. We compared patterns of habitat selection by badgers at three 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* (Ord, 1815)). At a coarse 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 with the resources available. Our study provides additional evidence that badgers behave as specialists when burrowing rodents are highly concentrated and predictable over space and time.

Key words: American badger, black-tailed prairie dog, *Cynomys ludovicianus*, generalist, space use, specialist, *Taxidea taxus*.

Résumé : Distinguer les espèces sur la base de l'ampleur relative de leur niche est une approche répandue en écologie des communautés qui peut améliorer la compréhension des liens entre les espèces et leurs milieux. Si une espèce peut présenter une écologie généralisée à l'échelle de son aire de répartition, les individus peuvent se comporter comme des spécialistes à l'échelle locale. Les blaireaux d'Amérique (*Taxidea taxus* (Schreber, 1777)) sont des carnivores terrestres décrits le plus souvent comme étant des généralistes. Nous avons comparé les habitudes de sélection d'habitats par les blaireaux à trois échelles différentes pour vérifier l'hypothèse voulant que ces animaux présentent des comportements concordant plus avec ceux de spécialistes qu'avec ceux de généralistes quand ils habitent des paysages comprenant des chiens-de-prairie à queue noire (*Cynomys ludovicianus* (Ord, 1815)). À échelle grossière, les blaireaux choisissent des colonies de chien-de-prairie à la grandeur du paysage. À échelle intermédiaire, nous avons documenté une utilisation significativement plus grande de colonies de chiens-de-prairie au sein des domaines vitaux des blaireaux. À échelle fine à l'intérieur de colonies, les blaireaux utilisent les secteurs ayant des densités relativement fortes de terriers de chien-de-prairie, où les proies sont vraisemblablement abondantes. À plusieurs échelles, les blaireaux font une utilisation étroite des ressources comparativement aux ressources disponibles. L'étude fournit de nouveaux indices du comportement de spécialiste des blaireaux quand des rongeurs fouisseurs sont en forte concentration et que leur présence est prévisible dans l'espace et le temps. [Traduit par la Rédaction]

Mots-clés : blaireau d'Amérique, chien-de-prairie à queue noire, *Cynomys ludovicianus*, généraliste, utilisation de l'espace, spécialiste, *Taxidea taxus*.

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, whereas 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, and risk of predation (Colwell and Fuentes 1975). 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 behave as a generalist when its ecology across its entire range is considered, some populations may behave as specialists locally (Fox and Morrow 1981; Bolnick et al. 2003).

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American badgers (*Taxidea taxus* (Schreber, 1777)) 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; Quaipe 1978; Minta 1992). Nonetheless, across their geographic range, badgers prey on a diversity of species in a wide range of habitats. Badgers use a variety of habitat types including grasslands, sagebrush-steppe, open forests, intermountain valleys, and agricultural fields (Messick and Hornocker 1981; Newhouse and Kinley 2000; Apps et al. 2002; Collins et al. 2012; Duquette et al. 2014; Kinley et al. 2014), and consume a diversity of food items such as mammals, birds, reptiles, amphibians, fish, insects, arthropods, carrion, eggs, and vegetation (Messick and Hornocker 1981; Warner and ver Steeg 1995; Goodrich and Buskirk 1998; Sovada et al. 1999; Newhouse and Kinley 2000). Characterization of habitat use by badgers has ranged from “prairie obligate” (Duquette et al. 2014) to “generalist, nonobligate species” (Paulson 2007). Within the context of diet or food habits, descriptions have ranged from “opportunistic foragers” (Lampe 1982; Sovada et al. 1999; Collins et al. 2007) to “strict carnivores” (Messick and Hornocker 1981). The dissimilar characterizations of badgers likely reflect 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 resource use 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 (species of the genus *Cynomys* Rafinesque, 1817) complexes across three spatial scales to test the hypothesis that badgers would behave as specialists when foraging on black-tailed prairie dogs (*Cynomys ludovicianus* (Ord, 1815)). At a course scale, 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 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* (Audubon and Bachman, 1851)), 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, 2011b).

Materials and methods

Study area

We conducted our field study from 2008 to 2010 on the Lower Brule Indian Reservation and Buffalo Gap National Grasslands, located approximately 250 km apart in central and southwestern South Dakota, USA, respectively. Both sites are considered mixed-grass prairie and have extensive populations of black-tailed prairie dogs (Schroeder 2007; Livieri and Anderson 2012; Grassel et al. 2015).

Badger capture and monitoring

To locate badgers for capture, we searched prairie dog colonies and adjacent noncolony habitat (≤ 0.3 km) that could be viewed from the colony edges at night while driving vehicles and using roof-mounted spotlights. When a badger was detected, leg-hold traps (#3 coil spring; Victor Soft Catch, Woodstream Corp., Lititz,

Pennsylvania, USA) were set at the entrance of occupied burrows. Captured individuals were chemically immobilized with an intramuscular injection of ketamine hydrochloride and xylazine hydrochloride (15 mg/kg body mass and 1.5 mg/kg, respectively; Goodrich and Buskirk 1998) and fitted with a harness-style radio transmitter (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). All animal use methods were approved by the University of Idaho Animal Care and Use Committee (#2008-26), followed animal care guidelines (Sikes et al. 2016), and permitted by the state of South Dakota (scientific collector permit # 1, 2 October 2007) and the Lower Brule Sioux Tribe (letter dated 28 August 2007).

We monitored badgers year-round at Lower Brule and seasonally at Buffalo Gap. The majority of monitoring occurred while simultaneously conducting spotlight surveys at night for black-footed ferrets on prairie dog colonies. Monitoring occurred during November 2008 – November 2010 at Lower Brule, and August–November 2008 and May–November 2009 at Buffalo Gap. We did not make comparisons across study sites (i.e., Lower Brule badgers vs. Buffalo Gap badgers). Therefore, we did not restrict our analyses to only the time periods when monitoring occurred simultaneously. 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. We considered juveniles as adults on 1 April of the year after their birth. Badgers were infrequently located more than once per day. In our analysis, we used only one badger location collected per day. We did not include locations of badgers collected during periods of extended inactivity associated with subfreezing temperatures to minimize serial autocorrelation (Minta 1992, 1993).

Prairie dog colony and burrow mapping

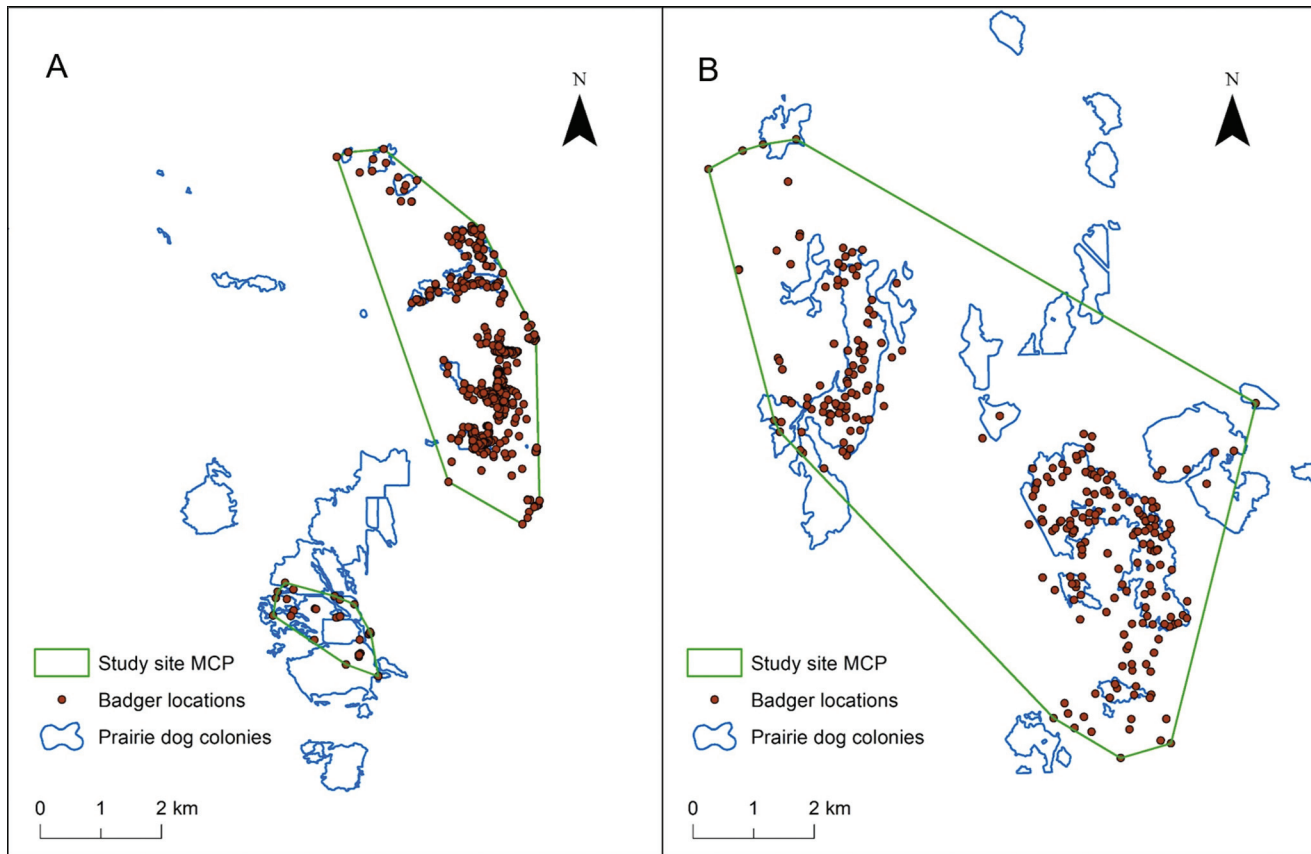
We mapped prairie dog colonies at Lower Brule in August 2007 and personnel of the U.S. Forest Service mapped colonies at Buffalo Gap during May–September 2007 using Trimble® GeoXM™ GPS receivers (1 m accuracy) while driving an ATV or walking along the perimeters of the colonies. Edges of colonies were distinguished by the distinct difference in vegetation height caused by foraging and vegetation clipping behavior of black-tailed prairie dogs (Koford 1958; Hoogland 1995). Burrow openings were mapped using Trimble® GeoXM™ GPS receivers on a subset of colonies at the Lower Brule site during July–August 2010. We imported data into ArcGIS version 9.3 (ESRI, Inc., Redlands, California, USA) to delineate resource availability and to conduct spatial analyses.

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 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 two 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 com-

Fig. 1. Locations of radio-marked American badgers (*Taxidea taxus*) on (A) the Lower Brule Indian Reservation ($n = 10$) and (B) the Buffalo Gap National Grasslands ($n = 12$), South Dakota, USA, during 2008–2010. The study site (available habitat) was delineated by creating a minimum convex polygon (MCP) from badger locations.



pared the proportion of badger locations recorded “on” prairie dog colonies to “off” prairie dog colonies using binomial proportion Z tests. Our analysis was a one-tailed test because our test reflected our hypothesis that badgers would use prairie dog colonies in greater proportion than their availability. If badgers used habitat in the proportion to its availability, then we would expect the proportion of locations on prairie dog colonies to be similar to the proportion of prairie dog colonies within the study area. We also tested for differences between sex and age categories using χ^2 tests.

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 ≥ 27 locations to estimate the relative intensity of use across space within the home range (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% UD with a grid cell size of $30 \text{ m} \times 30 \text{ m}$ using the Hawth’s Tools extension (Beyer 2004) in ArcGIS and Animal Space Use version 1.3 (Horne and Garton 2009). To evaluate resource use within the home range, we compared the proportions of the volume (three-dimensional) and area (two-dimensional) of the UD that overlapped colonies using a paired Z test. If badgers used the area within their home ranges equally, then we would not expect a difference in the proportion of volume and area within prairie dog colonies. 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 subset 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 telemetry locations of badgers and on available locations (sensu Biggins et al. 2006b) generated using the Hawth’s Tools extension (Beyer 2004) in ArcGIS that were cast randomly 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 available plots using a general linear mixed model with a repeated measure on individual badgers using Proc Mixed in SAS version 9.3 (SAS Institute Inc., Cary, North Carolina, USA). Colony and location (used or available) were treated as fixed effects. Our analyses were one-tailed tests because we hypothesized that badgers would select for areas within prairie dog colonies that have high densities of burrows at fine scales.

Results

Prairie dog colonies comprised relatively small portions of the total area used by badgers at our study sites (Figs. 1A, 1B). The Lower Brule MCP contained 522.2 ha of prairie dog colonies and 2438.1 ha of noncolony habitat. The Buffalo Gap MCP included 2401.3 ha of prairie dog colonies and 9455.4 ha of noncolony 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 (mean = 38.7 locations per individual, range = 4–99 locations per individual, SD = 25.3 locations per individual). At Lower Brule, radio-marked badgers ($n = 10$) used 11 of 11 prairie

Table 1. Characteristics of a subset of black-tailed prairie dog (*Cynomys ludovicianus*) colonies used by eight American badgers (*Taxidea taxus*) on the Lower Brule Indian Reservation, South Dakota, USA, during 2010.

Colony	Size (ha)	No. of burrows	No. of burrows/ha
Cattle Guard	9	3797	439.2
Sheldon South	7	3138	432.4
Sheldon East	3	854	290.3
High Otter	12	3079	265.8
Badger Head	13	3321	259.1

dog colonies that were located within the study area MCP that averaged 31 ha in size (range = 1–208 ha, SD = 62 ha). At Buffalo Gap, marked badgers ($n = 12$) used eight colonies that averaged 100 ha in size (range = 2–285 ha, SD = 120 ha). Eight colonies within the study area MCP were not used by marked badgers that averaged 23 ha in size (range = 2–45 ha, SD = 16 ha). Densities of prairie dog burrows averaged 337.4/ha (range = 259.1–439.2/ha, SD = 90.6/ha) on five prairie dog colonies at Lower Brule included in our fine-scale analyses (Table 1).

Badgers in our study selected for prairie dog colonies at the broadest spatial scale that 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%; $\chi^2 = 0.131$, $P = 0.718$), so data from both sites were combined for this component of our analyses. Badgers ($n = 22$) were located on prairie dog colonies during a mean of 66.9% of telemetry locations (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 (Figs. 1A, 1B; $Z = 34.23$, $P < 0.001$). 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%; $\chi^2 = 5.18$, $P = 0.023$), selection for prairie dog colonies was evident for both sexes (female: $Z = 26.99$, $P < 0.0001$; males: $Z = 21.22$, $P < 0.001$; Fig. 2A). Similarly, the proportion of locations on prairie dog colonies was significantly greater for adult badgers (70.6%, SE = 1.8%) compared with 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: $Z = 14.42$, $P < 0.001$; Fig. 2B).

Badgers also selected for prairie dog colonies at intermediate scales within home ranges. We generated UD_s 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 UD_s were created for each age class), for which 726 locations were recorded (mean = 45.4, range = 27–92, SD = 20.7). Size of 95% UD_s averaged 256.8 ha and ranged from 16.7 to 1396.5 ha (SD = 344.9 ha; Table 2). The proportion of the volume of 95% UD_s within prairie dog colonies (mean = 51.7%, range = 23.5–73.9%, SE = 4.2%) was significantly greater than the proportion of area of badger UD_s within prairie dog colonies (mean = 37.8%, range = 11.8–63.4%, SE = 4.2%; $Z = 6.09$, $P < 0.001$; Figs. 3A, 3B, and 4). 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 with a mean number of 39.6 within available plots ($n = 196$, range = 0–101, SE = 1.43). Areas used by badgers were associated with higher densities of burrows than available plots ($F_{[1,382]} = 5.80$, $P = 0.017$; Fig. 5). This pattern was relatively consistent across colonies (location \times colony interaction; $F_{[1,382]} = 1.86$, $P = 0.117$), suggesting that selection for

Fig. 2. Proportion of American badger (*Taxidea taxus*) locations ($n = 852$) recorded on colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) by sex (A) and age (B) categories from badgers radio-marked ($n = 22$) on the Lower Brule Indian Reservation, South Dakota, USA, and Buffalo Gap National Grasslands, South Dakota, USA, during 2008–2010. Horizontal line represents the proportion of prairie dog colonies within the study sites. Error bars represent standard error.

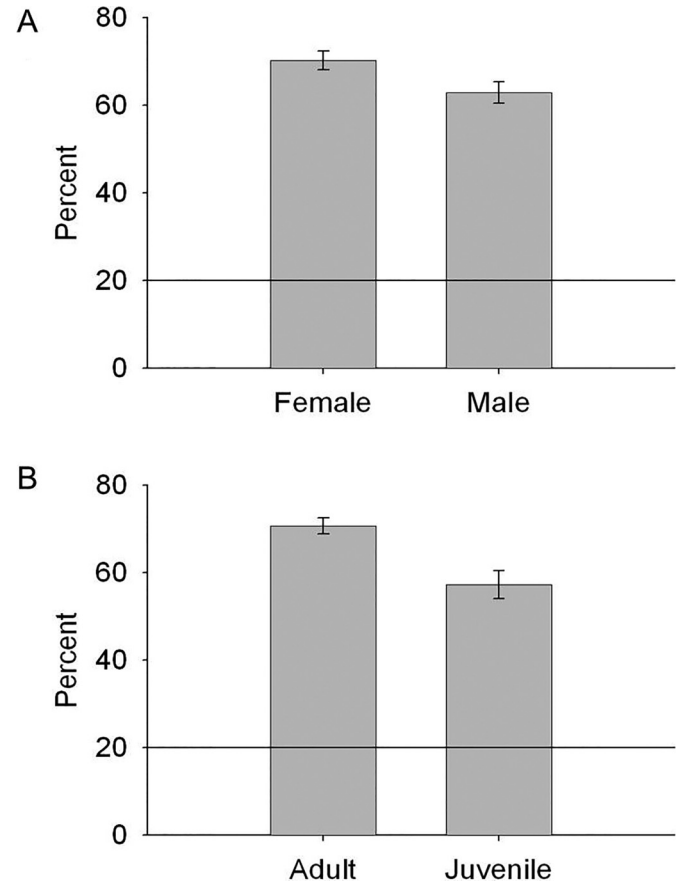
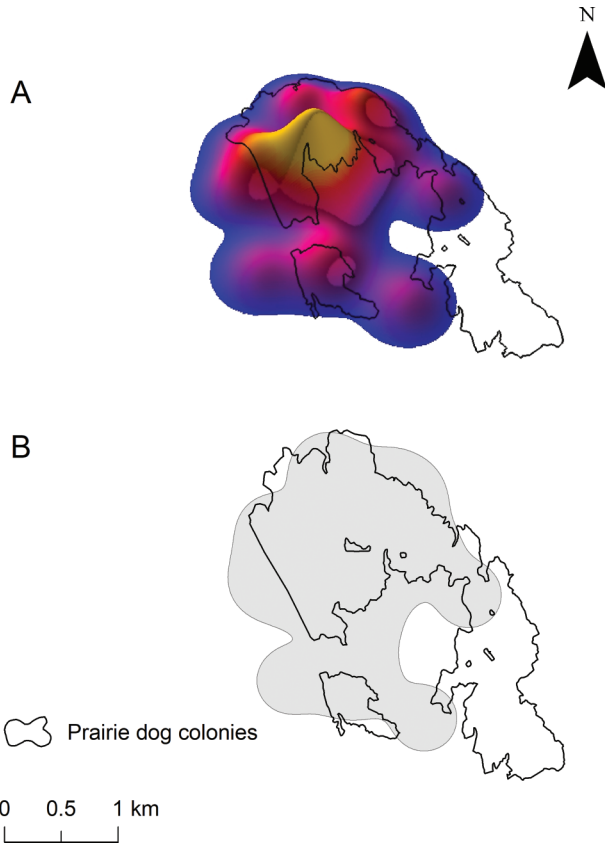


Table 2. Utilization distributions (UD) of American badgers (*Taxidea taxus*) using 95% fixed kernel estimators by sex and age on the Buffalo Gap National Grasslands, South Dakota, USA (2008–2009), and the Lower Brule Indian Reservation, South Dakota, USA (2008–2010).

ID	Study site	No. of locations	Sex	Age	UD (ha)
962	Buffalo Gap	40	Female	Adult	186.4
944	Buffalo Gap	29	Female	Adult	416.2
923	Buffalo Gap	28	Female	Adult	191.9
503	Buffalo Gap	32	Male	Adult	1396.5
483	Buffalo Gap	27	Male	Adult	536.6
863	Buffalo Gap	27	Male	Adult	483.8
583	Lower Brule	40	Female	Adult	147.9
781	Lower Brule	73	Female	Adult	26.4
843	Lower Brule	92	Female	Adult	66.4
742	Lower Brule	35	Female	Adult	210.1
054	Lower Brule	56	Female	Juvenile	66.5
742	Lower Brule	47	Female	Juvenile	16.7
722	Lower Brule	84	Male	Adult	152.7
604	Lower Brule	29	Male	Juvenile	144.1
032	Lower Brule	45	Male	Juvenile	42.5
683	Lower Brule	42	Male	Juvenile	24.5

Fig. 3. An example of a comparison between the proportion of volume (A) and area (B) of an American badger (*Taxidea taxus*) utilization distribution (UD) overlapping colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) at the Buffalo Gap National Grasslands, South Dakota, USA, during 2009. Warmer colors of the UD represent areas with higher probability of use, whereas cooler colors represent areas with lower probability of use.



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 they focused use within colonies on areas with relatively high densities of prairie dog burrows. Although American badgers have a broad functional niche across their geographic range, in our study areas, they exhibited strong selection for a relatively narrow range of habitat resources. The strong selection for prairie dogs at multiple scales represents a behavioral pattern that is more characteristic of a habitat and dietary 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 colonies of white-tailed prairie dogs (*Cynomys leucurus* Merriam, 1890) (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-

Fig. 4. Mean percent volume and area of American badger (*Taxidea taxus*) utilization distributions (UDs; $n = 15$) within colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation, South Dakota, USA, and Buffalo Gap National Grasslands, South Dakota, USA, during 2008–2010. Error bars represent standard error.

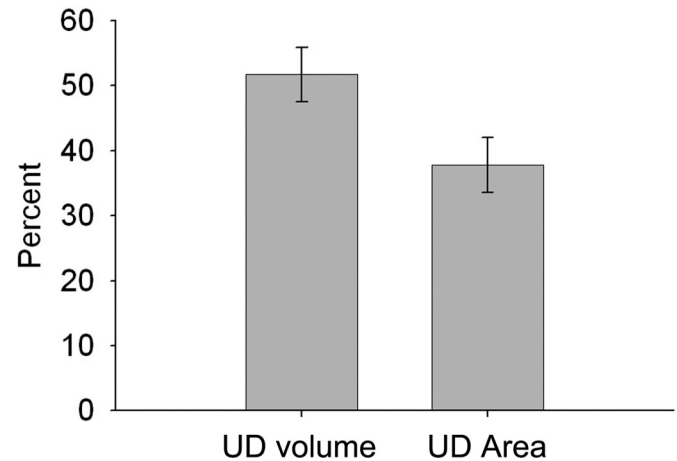
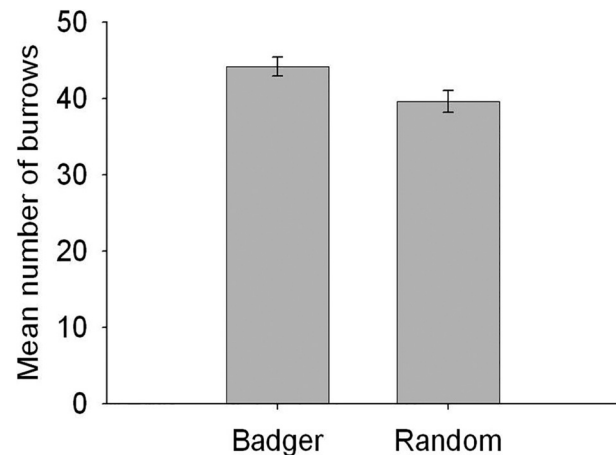


Fig. 5. Mean number of black-tailed prairie dog (*Cynomys ludovicianus*) burrows within 0.13 ha circular plots centered on American badger (*Taxidea taxus*; $n = 196$) and random ($n = 196$) locations on the Lower Brule Indian Reservation, South Dakota, USA, during 2008–2010. Error bars represent standard error.



use patterns. The spatial organization of female badgers is shaped largely by the distribution of food resources, whereas 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) reported five out of nine female badgers were located only 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 (Figs. 1A, 1B). The abundance of prey drives patterns of habitat selection for many predators including least weasels (*Mustela nivalis* Linnaeus, 1766) (Erlinge 1974; Klemola et al. 1999), a specialist of voles (species of the genus *Microtus* Schrank, 1798) (King and Moors 1979), and Canada lynx (*Lynx canadensis* Kerr, 1792) (Murray et al.

1994), a specialist of snowshoe hares (*Lepus americanus* Erxleben, 1777) (O'Donoghue et al. 1998). The unequal use of space within the badger home ranges and the disproportionate use of prairie dog colonies at our study sites supports the contention that availability of concentrated burrowing prey is resulting in strong selection for prairie dog habitats.

Within prairie dog colonies used by badgers, individuals also selected for areas that had high densities of prairie dog burrows and presumably relatively 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 creating their own burrows for shelter. Shearing hardened soils and pushing loosened soil is energetically costly for subterranean organisms such as the Botta's pocket gopher (*Thomomys bottae* (Eydox and Gervais, 1836)) (Vleck 1979) and degu (*Octodon degus* (Molina, 1782)) (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 compared with 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.

The results of our fine-scale analysis of badger use of prairie dog colonies are similar to selection patterns of black-footed ferrets, an extreme 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), which often positively correlate with densities of prairie dog prey (Biggins et al. 1993, 2006b). 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 that ferrets consume a broader range of prey items than previously acknowledged. 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 stomach and fecal samples from badgers. We suggest that similarity in fine-scale patterns of habitat selection and diets of ferrets and badgers also supports the contention that badgers in our study exhibited local specialization on prairie dogs.

The strong selection for prairie dog colonies by badgers in our study contrasts the association between prairie dog colonies and swift fox (*Vulpes velox* (Say, 1823)), a short-grass 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, then we would expect similar selection patterns by badgers. The contrasting use of prairie dog colonies between swift foxes and badgers, two species that are often considered to be generalists, lends support to our characterization that badgers behave as prairie dog specialists at our study sites.

All badgers in our study were captured on prairie dog colonies, which could have potentially biased our results. Perhaps badgers captured off of prairie dog colonies would have exhibited weaker selection of prairie dogs. We searched for badgers to capture off of prairie dog colonies, but none were observed and fresh diggings

were much less abundant compared with prairie dog colonies, although taller vegetation might have limited detection. Our results might also be biased by not detecting signals from badgers that moved long distances from prairie dog colonies and (or) whose signals were blocked by adjacent rugged terrain. We attempted to minimize this source of bias by using vantage points and traveling throughout our study areas when monitoring badgers. We did not limit monitoring to only prairie dog colonies.

Specialization on prairie dogs by badgers could have ecological consequences for endangered black-footed ferrets, including intraguild predation. Coexistence between the species could be facilitated by temporal or spatial avoidance of badgers by ferrets. Indeed, at our study sites, adult female badgers were avoided by ferrets, especially adult female ferrets (Grassel et al. 2015). However, other investigators have reported that badgers are actively attracted to areas used by ferrets and selectively excavate burrows in areas recently used by ferrets (Eads et al. 2013). In the absence of avoidance strategies, coexistence of ferrets and badgers at fine spatial scales would likely be facilitated, in part, by the relatively higher foraging efficiency of ferrets on prairie dogs compared with badgers (i.e., exploitative competition) and by selection of burrow systems with multiple openings, which likely lowers the risk of predation by badgers (Biggins 2012; Eads et al. 2016). Although ferrets are sometimes killed by badgers (Biggins et al. 1999, 2006a, 2011a), mechanisms appear to exist that facilitate the co-occurrence of these two species, one an obligate specialist and the other a facultative specialist on prairie dogs.

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, USA, was associated with high densities of plains pocket gophers (*Geomys bursarius* (Shaw, 1800)). Similarly, the abundance and distribution of badgers was related to concentrations of Belding's ground squirrels (*Urocyon beldingi* (Merriam, 1888)) in an agriculturally developed, semiarid area of southern Idaho, USA (Todd 1980). In British Columbia, Canada, badgers used agricultural lands, grasslands, and open forests, which were associated with the distribution of Columbian ground squirrels (*Urocyon columbianus* (Ord, 1815)) (Newhouse and Kinley 2000; Kinley et al. 2014). Proulx (2016) reported that badgers focused their activities in sites with a greater abundance of Richardson's ground squirrels (*Urocyon richardsonii* (Sabine, 1822)). 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) suggest 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* (Linnaeus, 1758)) sometimes specialize on earthworms (species of the genus *Lumbricus* Linnaeus, 1758) (Kruuk and Parish 1981), olive fruits (*Olea europaea* L.) (Kruuk and de Kock 1981), or young European rabbits (*Oryctolagus cuniculus* (Linnaeus, 1758)) (Martin et al. 1995, but see Revilla and Palomares 2002). Red foxes (*Vulpes vulpes* (Linnaeus, 1758)) 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, whereas 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 provided by 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, consequently, abundant prey. We suggest badgers that exhibit local specialization on prairie dogs could aptly be characterized as “facultative resource specialists” because badgers act as specialists on prairie dogs along both habitat and dietary axes.

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