Habitat Selection by Female Swift Foxes (*Vulpes velox*) During the Pup-Rearing Season

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ABSTRACT The swift fox (*Vulpes velox*) was historically distributed in western South Dakota including the region surrounding Badlands National Park (BNP). The species declined during the mid-1800s, largely due to habitat loss and poisoning targeted at wolves (*Canis lupis*) and coyotes (*C. latrans*). Only a small population of swift foxes near Ardmore, South Dakota persisted. In 2003, an introduction program was initiated at BNP with swift foxes translocated from Colorado and Wyoming. We report on habitat use by female swift foxes during the pup-rearing season (May–July) in 2009. Analyses of location data from 13 radiomarked female foxes indicated disproportional use ($P < 0.001$) of some habitats relative to their availability within swift fox home ranges. Swift foxes used grassland ($\hat{w} = 1.01$), sparse vegetation ($\hat{w} = 1.43$) and prairie dog towns ($\hat{w} = 1.18$) in proportion to their availability, whereas they were less likely to use woodland ($\hat{w} = 0.00$), shrubland ($\hat{w} = 0.14$), pasture/agricultural-land ($\hat{w} = 0.25$) and development ($\hat{w} = 0.16$) relative to availability. Swift foxes typically are located in habitats that provide greater visibility, such as shortgrass prairie and areas with sparse vegetation; which allow detection of approaching coyotes (e.g., primary predator of swift foxes).

KEY WORDS Badlands, habitat selection, South Dakota, swift fox, *Vulpes velox*

Swift foxes (*Vulpes velox*) inhabit shortgrass and mixed-grass prairies of the Great Plains of North America (Egoscue 1979). Historically, this small (~ 2 kg) fox occurred in parts of North Dakota, South Dakota, Montana, Nebraska, Wyoming, Colorado, Kansas, Oklahoma, New Mexico, and Texas, and the southern prairie region of Alberta, Manitoba, and Saskatchewan (Hall and Kelson 1959, Hall 1981, Samuel and Nelson 1982, Scott-Brown et al. 1987, Sovada and Scheick 1999). Swift foxes were once abundant throughout much of their range but had declined dramatically by the late 1800s (Zumbaugh and Choate 1985). Decline in swift fox abundance was attributed to conversion of native prairie to agriculture and associated declines in prey species, unregulated hunting and trapping, and predator control programs aimed at larger carnivores (Kilgore 1969, Egoscue 1979, Carbyn et al. 1994, Allardyce and Sovada 2003). Swift fox population declines were most severe in the southern and northern periphery of the species' range (Allardyce and Sovada 2003).

The present distribution of swift foxes includes a fragmented population extending from southern Wyoming through eastern Colorado, western Kansas, eastern New Mexico, Oklahoma panhandle, northern Texas, South Dakota and Nebraska, Canada, and Northern Montana (Carbyn 1998, Swift Fox Conservation Team 2000, Zimmerman et al. 2003). A reintroduction program was initiated in Badlands National Park and the surrounding area in South Dakota. From 2003 to 2006, 114 swift foxes were translocated from Colorado and Wyoming to Badlands National Park.

Little is known about habitat selection of female swift foxes in western South Dakota. Hence, the objective of our study was to evaluate habitat selection of female swift foxes during the pup-rearing season in western South Dakota. Swift fox breeding begins within the months of March and April in the study area. Previous studies (Russell 2006, G. M. Schroeder, Badlands National Park, unpublished data) indicated that swift fox selected habitats of short structure allowing long-distance visibility and areas nearer to prairie dog towns, roads and water bodies. These habitat features likely increased potential for the capture of prey and improved the ability of swift fox to detect approaching coyotes (*Canis latrans*); the primary cause of swift fox mortality (Allardyce and Sovada 2003). Based on previous results, we hypothesized that during the pup-rearing period, female swift foxes would select habitat types with high visibility and located near to prairie dog towns, which would provide constant and readily available food.

STUDY AREA

Badlands National Park (BNP) is located in southwestern South Dakota (Fig.1). The 1,846-km² study area included the north unit of BNP and surrounding area (Schroeder 2007). Twenty-three percent of the area was managed by the National Park Service, 34% by United States Forest Service,

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and 43% was privately owned (Fig. 2); <1% of the study area was used for row-crop agriculture (Schroeder 2007). The major industry in the region was livestock production; thus, the majority of the study area outside of BNP was grazed by cattle (Schroeder 2007). Within BNP, moderate- to low-intensity grazing by bison (*Bison bison*) occurred in 52% of the north unit; substantial grazing did not occur in the remaining 48% of the north unit (Schroeder 2007).

Mean annual temperature and precipitation in this region of South Dakota was 10.1° C and 40 cm, respectively (Fahnestock and Detling 2002) with dramatic seasonal variation, which is typical of the continental climate. Minimum and maximum temperature varied between −40° C and 47° C. Topography of the region was diverse and elevation ranged from 691 to 989 m above mean sea level (Russell 2006). The area within BNP was typified by highly eroded cliffs and spires over 100 m in height. Outside BNP, the terrain was less rugged and typified by rolling prairies and a relatively flat area (e.g., Conata Basin; Russel 2006). Vegetation in the region was dominated by mixed grass prairie species including buffalograss (*Buchloe dactyloides*), western wheatgrass (*Pascopyrum smithii*), and prickly-pear cactus (*Opuntia polyacantha*); the region was mostly void of tree and brush species (Russell 2006). The Cheyenne and White rivers formed the western and southern boundaries of the study area, respectively.

Figure 1. Swift fox study area in Badlands National Park located in southwestern South Dakota, USA, May–July 2009.

METHODS

We captured swift foxes, early May 2009, with modified wire box traps (Model 108SS; Tomahawk Live Trap Co., Tomahawk, WI, USA) of dimensions 81.3 cm × 25.4 cm × 30.5 cm (Sovada et al. 1998), which we set in the evening and checked the following morning. We manually restrained foxes, determined sex, weighed, and recorded general body condition. We weighed captured swift foxes with a spring scale (model 80210; Pesola® Macro-Line Spring scale, Rebmattli 19, CH-6340 Baar, Switzerland, EU) and determined age of captured foxes with tooth wear. We noted lactation of captured female foxes by presence of swollen nipples and matted hair as evidence of suckling and later confirmed presence of pups by checking den sites for evidence or observations of pups. We fitted lactating females with Very High Frequency (VHF) radiocollars (model M1830, <40 g; Advanced Telemetry Systems, Isanti, MN, USA). Our animal handling methods followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and were approved by the Institutional Animal Care and Use Committee at South Dakota State University (Approval number 08-A039).

Because swift foxes are nocturnal, we monitored radiocollared foxes twice per night from dusk to dawn. We started monitoring foxes each day at approximately 2030 hours and completed monitoring at 0500 hours. We collected two locations per night for each fox at an interval of approximately 3 to 4 hours. To maintain temporal independence, we avoided collecting locations at the same time on two successive days for any individual. We collected telemetry locations by using a null-peak vehicle mounted antennae system, equipped with an electronic digital compass and GPS unit (Brinkman et al. 2002). We calibrated telemetry systems with transmitters in known locations (Cox et al. 2002). We obtained estimates of swift fox locations using 3–4 bearings collected within a 10 minute period (White and Garrot 1990, Kitchen et al. 2005). We used LOCATE III (Nams 2006) to estimate locations using a minimum of three azimuths for all fox locations. We excluded location estimates from home range analyses with 95% error ellipses ≥20 ha (Brinkman et al. 2005). We used ≥50 locations to estimate home ranges of individual foxes. Mean number of locations used to calculate home ranges was 64 (SE = 1.4, range 51–68) and we used only foraging locations for current analyses. We imported location estimates into ArcView (ESRI, Inc., Redlands, CA, USA) and used the Home Range Extension (HRE; Rodgers and Carr 1998) to calculate 95% home ranges during the pup-rearing season (May–July). Because estimated fox locations were clustered, we used the adaptive kernel method for home range calculation. We conducted Geographic Information Systems (GIS) analyses with ArcGIS 9.1 (ESRI, Redlands, CA, USA) and used NAD 83, UTM Zone 13N for all GIS data collection and analysis.

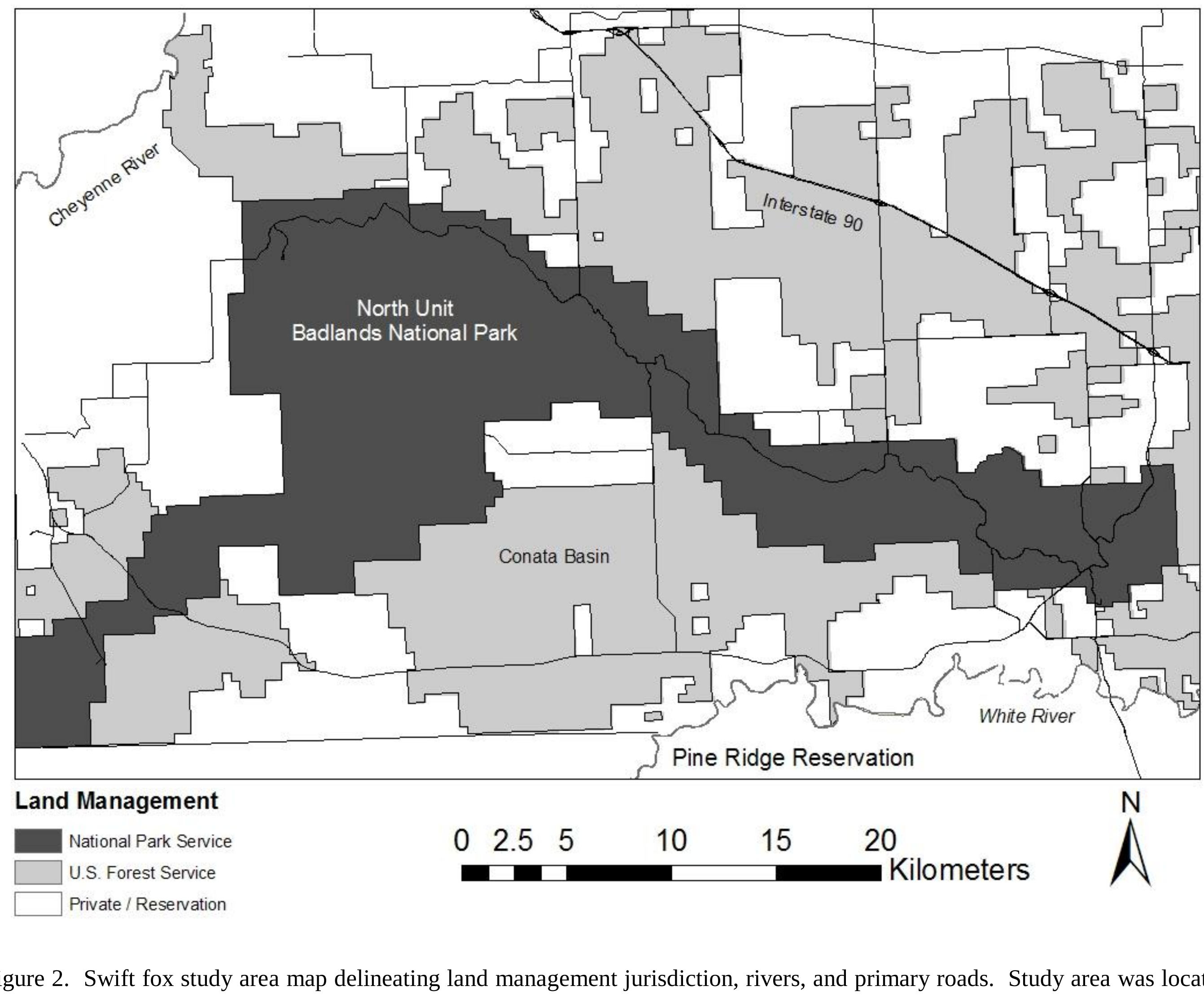

Figure 2. Swift fox study area map delineating land management jurisdiction, rivers, and primary roads. Study area was located in southwestern South Dakota, USA, May–July 2009.

We determined percentages of each habitat type available within individual fox home ranges from the USGS-NPS vegetation mapping of BNP (Loh et al. 1999). For resource selection analyses, habitat categories included grassland, shrubland, pasture/agricultural land, development, sparse vegetation, prairie dog towns, and woodlands. Grassland included the western wheatgrass grassland alliance, introduced grassland, blue grama (*Bouteloua gracilis*) grassland, little bluestem (*Schizachyrium scoparium*)-grama grassland-threadleaf sedge (*Carex filifolia*) grassland, 3-leaved sumac (*Rhus trilobata*)/threadleaf sedge shrub grassland, soap weed yucca (*Yucca glauca*)/prairie sand reed (*Calamovilfa longifolia*)/ shrub grassland; shrubland included western snowberry (*Symphoricarpos occidentalis*) shrubland, chokecherry (*Prunus virginiana*)-American plum (*P. americana*) shrubland, silver buffaloberry (*Shepherdia argentea*) shrubland, silver sagebrush (*Artemisia cana*)/western wheatgrass shrubland, sand sagebrush (*A. filifolia*)/prairie sand reed shrubland, sandbar willow (*Salix interior*) temporarily flooded shrubland; woodland was comprised of eastern cottonwood (*Populus deltoides*)/sandar willow woodlands, green ash (*Fraxinus pennsylvanica*)-American elm (*Ulmus Americana*) /chokecherry woodlands, Rocky Mountain juniper (*Juniperus scopulorum*)/ little seed rice grass (*Piptatherum micranthum*) woodland; pasture/agricultural land included cropland-pasture and other agricultural land; development was comprised of strip mines, quarries and gravel pits, mixed urban/built-up land, sandy-area beaches; sparse vegetation was comprised of only Badlands sparse vegetation complex whereas prairie dog (*Cynomys ludovicianus*) towns included only prairie dog town complexes. Row crop agricultural practices occur around BNP, which included alfalfa, winter wheat, and spring wheat, corn, soybean, millet, and oats. Planting and harvesting seasons varied according to the different types of row crops such as winter wheat (planted in the fall and harvested the subsequent summer) to corn (planted in spring and harvested in fall) to alfalfa (harvested one or more times from spring through fall).

We assessed habitat selection by comparing use and availability of habitat types at the individual home range level (Manly et al. 2002). Use was defined as animal locations in a particular habitat and availability was defined as the percentage of each habitat available at the individual home range level. We calculated selection ratios and chi-square values to estimate the overall deviation from random use of habitat types with program R version 2.8.1 (R Development Core Team 2009) and the adehabitat library (Calenge 2006). Selection ratios ($\hat{w}$) indicated habitat selection if they differed from 1 and were computed for each habitat type and each animal as the ratio of the used proportion to the available proportion (Calange and Dufour 2006). Selection for or against a habitat category was indicated if the confidence interval for $\hat{w}$ did not contain 1. Selection for the habitat category was indicated if the lower limit of $\hat{w}$ was >1, whereas selection against the habitat category was indicated if the upper limit of $\hat{w}$ was <1. Use in proportion to availability (neutral selection) was indicated if the confidence interval for $\hat{w}$ contained the value 1 (Manly et al. 2002). Eigenanalysis of selection ratios was performed to explain variation in selection of habitat type among animals (Calange and Dufour 2006). If all animals selected the same habitat types, then use of the first axis of the analysis explained most of the variation in habitat selection, whereas the method returns several axes if there is variability in habitat selection among monitored animals (Calange and Dufour 2006).

We generated equal numbers of random locations within the buffered Minimum Convex Polygon area of all fox locations, which we used to delineate the boundaries for habitat analysis. We performed logistic regression analysis with SYSTAT 11 (Wilkinson 1990) to fit an appropriate model to evaluate the influence of presence of prairie dog towns, water bodies, and roads on fox locations. We measured distances of fox and random locations to prairie dog towns, water bodies, and roads. We coded random locations as 0 and fox locations as 1 to run binary logistic regression for model evaluation. We calculated mean distance of actual fox locations and random locations from prairie dog towns, water bodies, and roads. We performed a paired *t*-test to compare whether distance from prairie dog towns, water bodies, and roads differed between swift fox and random locations at the 90% level of significance (alpha of $P \leq 0.10$). We determined vegetation height by sliding a 15-cm disc down a Robel pole (Robel et al. 1970) until it contacted any portion of a plant (Kennedy et al. 2001). We collected vegetation height at fox locations twice per week for comparison of habitat use by foxes for different vegetation heights. We collected vegetation heights at fox locations within 3 days of obtaining a VHF location estimate.

RESULTS

From May to July 2009, we monitored 14 female swift foxes and recorded 842 locations. Of the 14 female foxes, 4 were captured and radio-marked in 2009 and 10 were marked in previous years (2004 to 2008). We verified pup rearing for all 14 female foxes by observing pups at dens. The average 95% home range of female swift foxes during the pup-rearing season was 8.83 km^2 (SE = 1.32, 95% CI = 5.96–11.71).

Some habitats within the 95% home-range estimates were not used by individual swift foxes in proportion to availability ($\chi^2_1 = 73.43$, $P < 0.001$; Table 1). During the pup-rearing season, female foxes used grassland, sparse-vegetation, and prairie dog towns in proportion to availability, whereas they avoided woodlands, shrublands, development, and pasture/agricultural land (Table 2). Resource selection was assessed from data collected from 13 swift foxes as the home range of one individual was located outside the vegetation mapping area that we used for habitat analyses. Eigenanalysis of selection ratios was used to explain the variability in the data (Fig. 3). Sparsely vegetated habitat and prairie dog town habitat explained ~71% of the variability in individual animal habitat selection during the pup-rearing season. The first axis, which represented sparse vegetation, explained 42% of the variability, whereas the second axis, which represented prairie dog towns, explained 29% of the variability. Addition of the third factor, which was grassland vegetation, increased information explained to 88%.

Average distance of fox locations from prairie dog towns was 0.90 km (95% CI = 0.80–1.00); from water bodies it was 0.69 km (95% CI = 0.62–0.77), and from roads it was 2.2 km (95% CI = 2.08–2.32). Average distance of random locations from prairie dog towns was 0.81 km (95% CI = 0.76–0.87); from water bodies was 0.61 km (95% CI = 0.54–0.67); and from roads was 2.36 km (95% CI = 2.24–2.48). We were unable to develop a logistic regression that fit the distance data for fox and random locations. However, paired *t*-tests conducted between distances of fox locations and random locations to prairie dog towns (P = 0.003), water (P = 0.087), and roads (P = 0.067) indicated that swift foxes were closer to roads but farther from prairie dog towns and water sources than random distances. Average vegetation height of habitats used by foxes was 15.9cm (95% CI = 15.50–16.40). Lactating female foxes selected (χ_1^2 = 638.46, P < 0.001) locations with low vegetation height (71.8%) more than locations having medium (26.5%) and high (1.7%) vegetation heights.

Table 1. Percent availability and use of habitat types for lactating female swift fox during the pup-rearing season (May–July 2009) at Badlands National Park and surrounding areas, South Dakota.

Habitat	Available (%)	Use (%)
Grassland	70.8	75.0
Woodland	0.2	0.0
Shrubland	3.4	0.4
Pasture/agricultural land	3.4	0.9
Development	0.2	0.2
Sparse vegetation	9.4	9.4
PD towns[a]	12.6	14.6

[a] Prairie dog towns

Table 2. Estimated selection ratios, standard errors, and confidence intervals of selection for habitats of female swift foxes (n = 13) in Badlands National Park and surrounding areas during the pup-rearing season (May–July) of 2009 using design III (Manly et al. 2002) with known proportion of available resource units.

Habitat	Design III			
	Selection Index	SE	CI	
	($\hat{w}$)		Lower	Upper
Grassland	1.010	0.046	0.899	1.122
Woodland	0.000	0.000	0.000	0.000
Shrubland	0.139[-]	0.075	0.000[c]	0.322
Pasture[a]	0.254[-]	0.202	0.000[c]	0.750
Development	0.157[-]	0.215	0.000[c]	0.684
Sparse vegetation	1.426	0.298	0.697	2.156
PD town[b]	1.181	0.253	0.560	1.802

[a] Pasture includes agricultural land; [b] Prairie dog towns; [c] For shrubland, pasture, and development negative lower limit was changed to 0.000; [-] Indicates that the selection index ($\hat{w}$) is significantly different from 1 and the habitat is used less than expected from available.

DISCUSSION

Unfortunately, we were only able to collect data on female swift foxes during one pup-rearing period, which limits inferences from our study. Nevertheless, few data have been collected on habitat selection of swift foxes that have recolonized the northern portion of the historic distribution of the species via restoration efforts. Furthermore, our study was focused on a sample (*n* = 14) of females actively provisioning pups while using a variety of habitats. At the time of our study, this sample represented 27% of actively reproducing female swift foxes known to inhabit the area under study. Therefore, we believe our results provide a robust assessment of habitat selection during the pup-rearing period for female swift foxes occupying the Northern Great Plains.

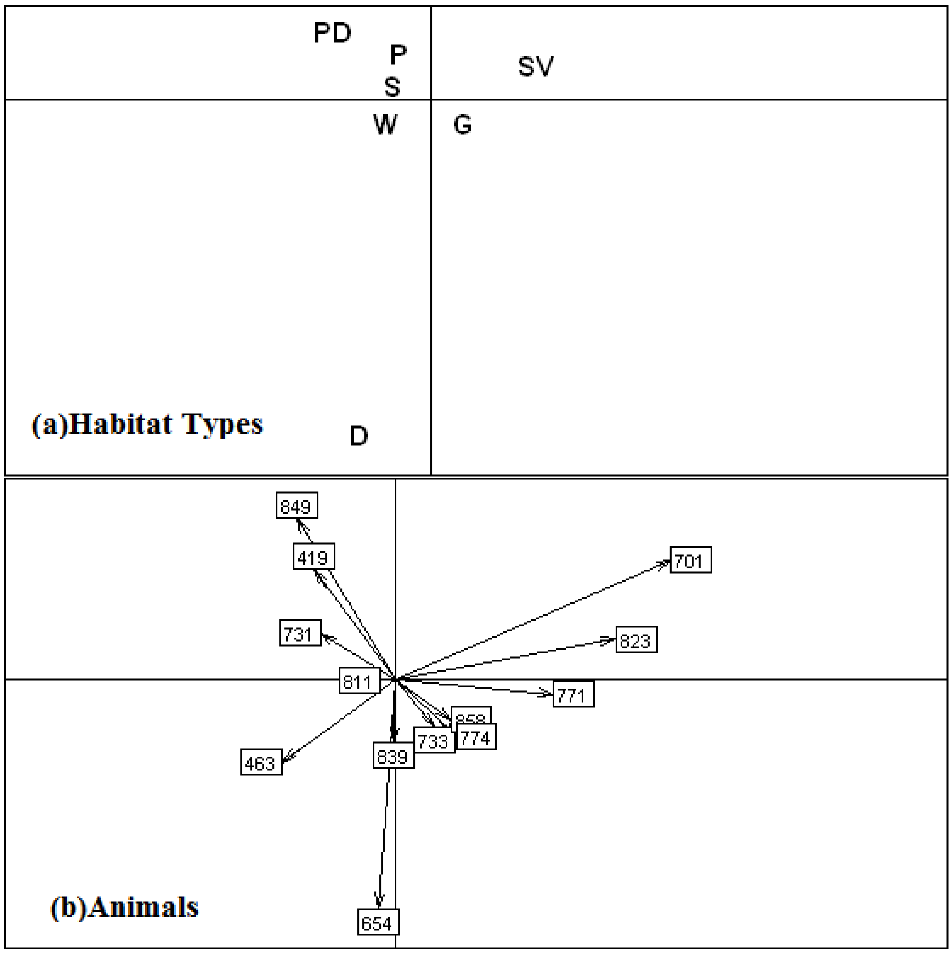

Figure 3. Results of the eigenanalysis of home-range level (design III; Manly et al. 2002) selection ratios conducted to highlight habitat selection by 13 lactating female swift fox on seven habitat types in Badlands National Park, South Dakota, USA, May–July2009. (a) Habitat type loadings on the first 2 factorial axes. (b) Animal scores on the first factorial plane. Vectors represent individual swift fox. PD = Prairie dog towns, P = Pasture/Agricultural land, S = Shrubland, G = Grassland, SV = Sparse vegetation, W = Woodlands, D = Development.

Habitat selection can be referred to as a hierarchical process of behavioral responses that result in the disproportionate use of habitats, and that influence survival and fitness of individuals (Jones 2001). Our study indicated that during the pup-rearing season (May–July), female swift fox avoided woodlands, shrublands, development, and pasture/agricultural land habitat types. Habitats are heterogeneous with ‘rich’ habitats, providing high survival and reproductive fitness to the organism, and ‘poor’ habitats, providing low survival and reproductive fitness (Rice and Owsley 2005). The definition of ‘rich’ habitat for swift fox is characterized by sparse vegetation of low height that provides greater visibility (Olson 2000, Harrison and Schmitt 2003, Russell 2006, Thomson and Gese 2007). Our results support previous research indicating that foxes select sparse vegetation. Swift foxes are opportunistic foragers

(Sovada et al. 2001) and feed on a variety of food resources (Harrison 2003), which may influence the variation in resource selection observed by female swift foxes during the pup-rearing season. The eigenanalysis indicated that all 3 axes were necessary to explain the resource selection of swift fox. Although most of the individuals used sparse vegetation, prairie dog towns and grassland vegetation types, some individuals also used pasture/agricultural land, shrubland, woodland, and development to a small extent. Among the individuals studied for habitat selection, those with limited access to 'rich' habitats, like grassland, sparse vegetation, and prairie dog towns, frequented pasture/agricultural land, shrubland, woodland, and development.

Swift foxes are restricted to areas west of the tallgrass prairies in central North America (Egoscue 1979, Scott-Brown et al. 1987). Swift fox select open vegetation with greater visibility to avoid predation from carnivores of larger body size (Thomson and Gese 2007), such as red fox (*V. vulpes*) and coyotes, which have been reported as a major cause of fox mortality (Kamler and Ballard 2002, Karki et al. 2007). Also, swift fox avoidance of habitat with tall vegetation was evident from our results that most locations were in low vegetation. In New Mexico, swift fox visited scent stations less than expected when grass height was >30 cm (Harrison and Schmitt 2003). Kamler (2003) reported that mean shoulder height of adult swift fox ranged from 29 to 30 cm. Thus, if the vegetation height is greater than a swift fox's shoulder height, visibility would be reduced. Low visibility increases vulnerability to coyote depredation (Kamler 2003).

Female swift foxes used locations that were farther away from prairie dog towns and water but closer to roads during the pup-rearing season than would be expected based on random points. These results are in accordance with previous research (Russell 2006) that indicated foxes selected locations closer to roads likely due to increased prey availability and decreased coyote predation (Almasi-Klausz and Carbyn 1999). Foxes do not depend on prairie dogs solely for their prey; however, use of prairie dog town habitat equivalent to availability indicate that prairie dogs provide increased access to both live prey and carrion during this critical period in the life history of the species (Nicholson et al. 2006). Russell (2006) documented a frequency of occurrence of 41.2% for prairie dogs in feces of swift foxes during summer 2005 in western South Dakota, which was at least twice the frequency of occurrence documented in spring seasons. Other factors that could affect swift fox use of prairie dog town habitat include the presence of golden eagles (*Aquila chrysaetos*) and coyotes.

During the pup-rearing season from May to July 2009, average home range size of female swift foxes within the Badlands ecosystem was 8.8 km^2. The smallest home-range for a female swift fox in our study was 1.4 km^2, whereas the largest home-range was 17.4 km^2. Variation in home-range size may be due to difference in age of individual foxes and habitat type within the home-range of individual foxes. For example, the fox with the smallest home range was approximately 5-years-old and inhabited an area that was comparatively closer to prairie dog towns (1.67 km) and water bodies (0.09 km) but was farther from roads (4.84 km) than that of other foxes. Conversely, the fox with the largest home range was approximately 2-years-old, was farther away from prairie dog towns (2.48 km) but was closer to roads (0.17 km) than other foxes. Consequently, older foxes might possess enough experience to select suitable habitat with easy access to prey. Also, older foxes might be more dominant over the younger individuals forcing them to possess lower quality habitat within their home ranges. Our sample size of age groups of female swift foxes did not allow statistical analysis that would provide support for this hypothesis. However, age structure of swift fox populations may be linked to population viability in regions with high road densities and fragmented suitable foraging habitat.

MANAGEMENT IMPLICATIONS

Habitat selection of female swift foxes that were rearing pups in and around Badlands National Park indicated that swift fox avoided habitats with tall vegetation such as agricultural land/pasture, shrublands, and woodlands and human-caused disturbances. Success of female swift fox in rearing pups plays a vital role in both long- and short-term viability of populations and is strongly related to habitat quality and availability, population demographics, and the genetic fitness of individuals. Managers can maintain suitable habitats for swift fox populations by manipulating the height of vegetation via grazing and/or mechanical methods like prescribed fire. Moreover, suitable habitats for swift fox during the pup-rearing season can be maintained by converting unfavorable vegetation types which were avoided by swift foxes like pasture/agricultural land, woodland, shrubland, and developed areas, into native grassland. Also, maintaining prairie dog towns will enhance suitable habitats for swift foxes during the pup-rearing season.

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