Home range size and resource use by swift foxes in northeastern Montana

Andrew R. Butler,* Kristy L.S. Bly, Heather Harris, Robert M. Inman, Axel Moehrenschlager, Donelle Schwalm, and David S. Jachowski

Prairie Ecology Lab, Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, USA (ARB, DSJ)
Northern Great Plains Program, World Wildlife Fund, Bozeman, MT 59715, USA (KLSB)
Montana Fish, Wildlife, and Parks, Glasgow, MT 59230, USA (HH)
Montana Fish, Wildlife, and Parks, Helena, MT 59620, USA (RMI)
Centre for Conservation Research, Calgary Zoological Society, Calgary, AB T2E 7V6, Canada (AM)
Department of Biology, University of Maine-Farmington, Farmington, ME 04938, USA (DS)

*Correspondent: abutle5@clemson.edu

Swift foxes (*Vulpes velox*) are endemic to the Great Plains of North America, but were extirpated from the northern portion of their range by the mid-1900s. Despite several reintroductions to the Northern Great Plains, there remains a ~350 km range gap between the swift fox population along the Montana and Canada border and that in northeastern Wyoming and northwestern South Dakota. A better understanding of what resources swift foxes use along the Montana and Canada border region will assist managers to facilitate connectivity among populations. From 2016 to 2018, we estimated the home range size and evaluated resource use within the home ranges of 22 swift foxes equipped with Global Positioning System tracking collars in northeastern Montana. Swift fox home ranges in our study were some of the largest ever recorded, averaging (± SE) 42.0 km^2 ± 4.7. Our results indicate that both environmental and anthropogenic factors influenced resource use. At the population level, resource use increased by 3.3% for every 5.0% increase in percent grasslands. Relative probability of use decreased by 7.9% and 7.4% for every kilometer away from unpaved roads and gas well sites, respectively, and decreased by 3.0% and 11.3% for every one-unit increase in topographic roughness and every 0.05 increase in normalized difference vegetation index (NDVI), respectively. Our study suggests that, to reestablish connectivity among swift fox populations in Montana, managers should aim to maintain large corridors of contiguous grasslands at a landscape scale, a process that likely will require having to work with multiple property owners.

Key words: conservation translocation, grasslands, reintroduction, resource utilization function, *Vulpes velox*

The swift fox (*Vulpes velox*) is a small canid, endemic to the short- and mixed-grass prairies of North America. Once abundant throughout the Great Plains, populations began to decline in the late 1800s due to rodent and predator control programs and the conversion of prairie to cultivated crop fields (Carbyn 1998). As a result, the species is currently recognized as a species of conservation concern over much of its range (Dowd Stukel 2011). In the Northern Great Plains, swift foxes were extirpated by the mid-1900s (Sovada et al. 2009) and the swift fox was listed as endangered in Canada in 1998 by the Committee on the Status of Endangered Wildlife in Canada and as threatened under the Species at Risk Act in 2012. In the United States, the swift fox was determined to warrant federal listing under the Endangered Species Act, but was precluded from listing due to lack of resources, and removed from the candidate list in 2001. There have been three reintroductions in Montana and Canada and four in South Dakota since the 1980's, all of which have established regional populations (Sasmal et al. 2015). Despite over 30 years elapsing since these reintroductions, there remains a range gap of approximately 350 km between the swift fox population along the Montana and Canada border and the population in northeastern Wyoming and northwestern South Dakota (Alexander et al. 2016).

Determining how much area a species needs to meet its life history requirements, and where suitable habitat is located, are essential aspects of creating sound strategies for enhancing population connectivity (Güthlin et al. 2011; Magg et al. 2016). Rather than wander nomadically, many animals restrict their movements to certain areas defined by Seton (1909) as home ranges. These home ranges, defined by Powell and Mitchell (2012) as "that part of an animal's cognitive map that it chooses to keep up-to-date with the status of resources (including food, potential mates, safe sites, and so forth) and where it is willing to go to meet its requirements (even though it may not go to all such places)," are important areas to delineate to better understand a species' ecology because they can illuminate important wildlife–habitat relationships. Previous estimates of swift fox home range size show that home range sizes can be quite variable, depending on geographic location. The average home ranges in Colorado were estimated to be 4.2–7.6 km^2 (Kitchen et al. 1999; Lebsock et al. 2012), whereas home ranges in Nebraska and Canada were estimated to be approximately 32.0 km^2 (Hines and Case 1991; Moehrenschlager et al. 2007), suggesting that home range size might vary by latitude (Table 1). However, there are only a few studies of home range size from the northern range of swift foxes (Hines and Case 1991; Moehrenschlager et al. 2007; Mitchell 2018). All previous studies used VHF tracking methods to gather locations for estimating home range size, which suggests that variability may be due to differences in tracking ability and effort. Additional studies on swift fox home range size in the Northern Great Plains will provide managers with a better understanding of the scale of swift fox home range size in this portion of its range, which will help them determine the appropriate scale at which management strategies must take place to be effective.

Contrasting patterns in the types of habitats selected for by swift foxes across their range also have been observed. Most of the past studies of second-order (selection of a home range), third-order (selection of a habitat patch within the home range), and fourth-order (selection of resources within a habitat patch), habitat selection (Johnson 1980) have found that swift foxes are grassland specialists that prefer short- and mixed-grass prairie habitats where grass is less than 30 cm tall, soil is soft, small mammals are abundant, terrain is flat, and shrub densities are low (Hines and Case 1991; Kitchen et al. 1999; Kamler et al. 2003a; Sovada et al. 2003; Russell 2006; Thompson and Gese 2007; Sasmal et al. 2011). These studies also found that they generally avoid agricultural fields, areas of grass greater than 30 cm tall, steep terrain, and areas of high shrub density (Harrison and Schmitt 2003; Kamler al. 2003a; Russell 2006; Thompson and Gese 2007; Sasmal et al. 2011). Swift foxes have been found to avoid areas with more prey, such as areas of high vegetative structural diversity, and select for areas with less prey, such as areas with low structural diversity (Thompson and Gese 2007). These resource use patterns are thought to be adaptations to reducing predation risk by increasing visual detection of predators, such as coyotes (*Canis latrans*), the main predator of swift foxes, and increasing access to dens, which swift foxes use daily as predator refuges.

There is an increasing anthropogenic footprint on the landscape in the northern portion of the range of the swift fox in the form of roads, cultivated crop fields, and oil and gas development, that might provide challenges for swift fox conservation, and particularly so for connecting the population on the Montana–Canada border with those in South Dakota and Wyoming (MTFWP 2019). Past studies on the effects of roads on swift fox ecology suggest that swift foxes may obtain some benefit from the presence of roads, such as using them for traveling and scavenging (Hines and Case 1991; Nevison 2017). Moreover, Cypher et al. (2009) found that two-lane roads did not have a significant negative impact on an ecologically similar species, the San Joaquin kit fox (*Vulpes macrotis mutica*). Contrary to most studies on the influence of crop fields on swift foxes, research in Kansas that compared swift fox ecology in agricultural versus rangeland-dominated areas, suggested that swift foxes might be tolerant of agricultural fields and use them under certain conditions (Sovada et al. 2003). While there are no published studies on the effects of oilfield development on swift foxes, previous research on the effects of oil development on San Joaquin kit foxes found that they use areas with low to medium levels of oil development (Warrick and Cypher 1998; Fiehler et al. 2017), and that at lower levels of development they do not alter their movements

Table 1.—Geographic location, home range estimator used in study, sample size used to estimate home range size, and average home range size (km^2) and standard error of swift foxes, *Vulpes velox*, in North America. Locations in the top part of the table are from the northern portion (>42°N) of the range and locations in the bottom part of the table are from the southern portion (<42°N) and are ordered from north to south.

Location	Home range estimator	Sample size	HR size	Citation
Canada	99% fixed kernel density	47	31.9 ± 4.8	Moehrenschlager et al. (2003)
Montana	99% fixed kernel density	23	42.0 ± 4.7	This study
Montana	95% fixed kernel density	23	29.4 ± 3.1	This study
South Dakota	95% kernel density	24	55.4 ± 5.8	Mitchell (2018)
Nebraska	100% minimum convex polygon	7	32.3 ± 9.8	Hines and Case (1991)
Wyoming	95% adaptive kernel density	10	11.7 ± 1.3	Pechacek et al. (2000)
NE Colorado	95% fixed kernel density	13	4.2 ± 0.8	Lebsock et al. (2012)
Kansas	95% adaptive kernel density	21	15.9 ± 1.6	Sovada et al. (2003)
SE Colorado	95% adaptive kernel density	73	7.6 ± 0.5	Kitchen et al. (1999)
Texas	95% adaptive kernel density	17	11.7 ± 1.0	Kamler et al. (2003a)
New Mexico	95% adaptive kernel density	6	21.9[a]	Harrison (2003)

[a]No SE reported.

or home range sizes (Zoellick et al. 2002). Providing managers with more information on swift fox resource use in the Montana and Canada border region could help to facilitate connectivity among disjunct populations by providing information to help guide habitat conservation and restoration efforts between populations.

In this study we addressed two main objectives: (1) to estimate the home range size of swift foxes in the Great Plains of northeastern Montana; and (2) to evaluate support for multiple competing hypotheses of how environmental conditions influence swift fox resource use. We hypothesized that home ranges would be larger than those in the southern portion of their range (Moehrenschlager et al. 2007). We hypothesized that swift fox resource use would be determined by den site availability, predation risk, and anthropogenic development. We predicted that the greater availability of potential den sites would be associated positively with resource use (Hines 1980; Olson 2000), while increased predation risk and anthropogenic development would negatively influence swift fox resource use within their home range (Kamler et al. 2003a; Thompson and Gese 2007). We assessed home range size and resource selection of swift foxes using data from Global Positioning System (GPS) collars. The data obtained allow for finer-scale investigations into animal movement behavior and resource utilization, a potentially important advancement in the understanding of the spatial ecology of swift foxes.

Materials and Methods

Study area.—We selected our study area to overlap the current southern edge of known swift fox distribution in northeastern Montana (Fig. 1A). At least 900 swift foxes were reintroduced into Canada, just north of this region, between 1983 and 1997 (Moehrenschlager and Moehrenschlager 2018). Based on subsequent monitoring through 2015, they have not expanded south into the United States beyond US Route 2 (Moehrenschlager and Moehrenschlager 2018). This lack of range expansion is a concern to regional managers and conservation organizations. We, therefore, chose to study swift foxes in the region where expansion has slowed. Specifically, our study area included northern Blaine, Phillips, and Valley, counties (Fig. 1B), totaling 17,991 km². The dominant vegetation types in the study area were native short-grass and mixed-grass prairie with areas of dryland agriculture, consisting mostly of wheat fields, and shrubland consisting mostly of sagebrush (*Artemisia* spp.). Irrigated agricultural fields were predominant along the southern boundary of the study area adjacent to US Route 2 and the Milk River. There were few paved roads in the study area; most roads were gravel and unimproved two-track trails through pastures. Topography consisted mostly of level to rolling terrain with some steeper coulees and elevations ranged from 629 to 1068 m. The climate of the study area was arid with the average annual precipitation ranging from 19 to 52 mm and average monthly temperature ranging from -1.8°C to 13.9°C (Zimmerman 1998).

Capture and monitoring.— We trapped swift foxes from October to December in 2016 and 2017 using 83 cm × 31 cm × 31 cm single-door and 109 cm × 39 cm × 39 cm double-door Tomahawk box traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) modified following Moehrenschlager et al. (2003). We baited traps with roadkilled white-tailed jack rabbit (*Lepus townsendii*), mule deer (*Odocoileus hemionus*), commercially available beef steak, as well as a commercially available trapping bait (Powder River, Minnesota Trapline Products, Pennock, Minnesota). We opened traps at sunset and checked and closed them at sunrise, and when night-time temperatures were less than 6°C, we checked traps at midnight as well. We weighed, measured, aged, and determined the sex of swift foxes without the use of chemical immobilization (Kamler et al. 2003a; Moehrenschlager et al. 2007; Thompson and Gese 2007). We classified swift foxes as adult or juvenile based on tooth wear and color (Ausband and Foresman 2007). We fitted swift foxes weighing greater than 2 kg with ~35 g GPS collars (LiteTrack30, Sirtrack, Havelock, New Zealand), which gave a collar weight of 1.75% or less of a swift fox's body mass. Handling procedures followed American Society of Mammalogists' guidelines (Sikes et al. 2016) and were approved by the Clemson University Institutional Animal Care and Use Committee (AUP2016-036) and Montana Department of Fish, Wildlife, and Parks (Scientific Collector's Permit 2016–107).

We programmed collars to attempt a GPS location every 2 h in October 2016– March 2017. In our second field season, October 2017–May 2018, in an attempt to extend the battery life of the collars in order to gather data across a 12-month period, we programmed collars to attempt a GPS location every 5 h for each individual. Given the differences in location rate between years of the study, we carried out *t*-tests to determine if there was a difference in the average number of days that swift foxes were monitored, and the average number of locations collected per swift fox between 2016 and 2017 and 2017 and 2018.

We tested the accuracy of GPS collars by simultaneously hanging two collars on strands of barbed wire approximately 45 cm off the ground. We marked the location of each test collar with a handheld GPS (Garmin GPSMAP 64, Olathe, Kansas). When processing the test locations, first we only used locations that had greater than three satellites, which provides higher accuracy than two dimensional locations from fewer satellites (Moen et al. 2016). Then we averaged the distance between the test collar location (from handheld GPS unit) and the GPS locations from the collar. Lastly, we plotted the dilution of precision (DOP) values against the average distance values and found that most locations with a DOP value equal to 10 had an average distance value of 30 m or less. Since our resource variable layers were at a 30 m resolution (see below), we used a DOP value of 10 as a cut-off when filtering locations. The average GPS error for test collar locations with three or more satellites and a DOP value of 10 or less (*n* = 460) was 6.7 m (range = 0.31–33.4 m). Therefore, when processing locations from collared animals,
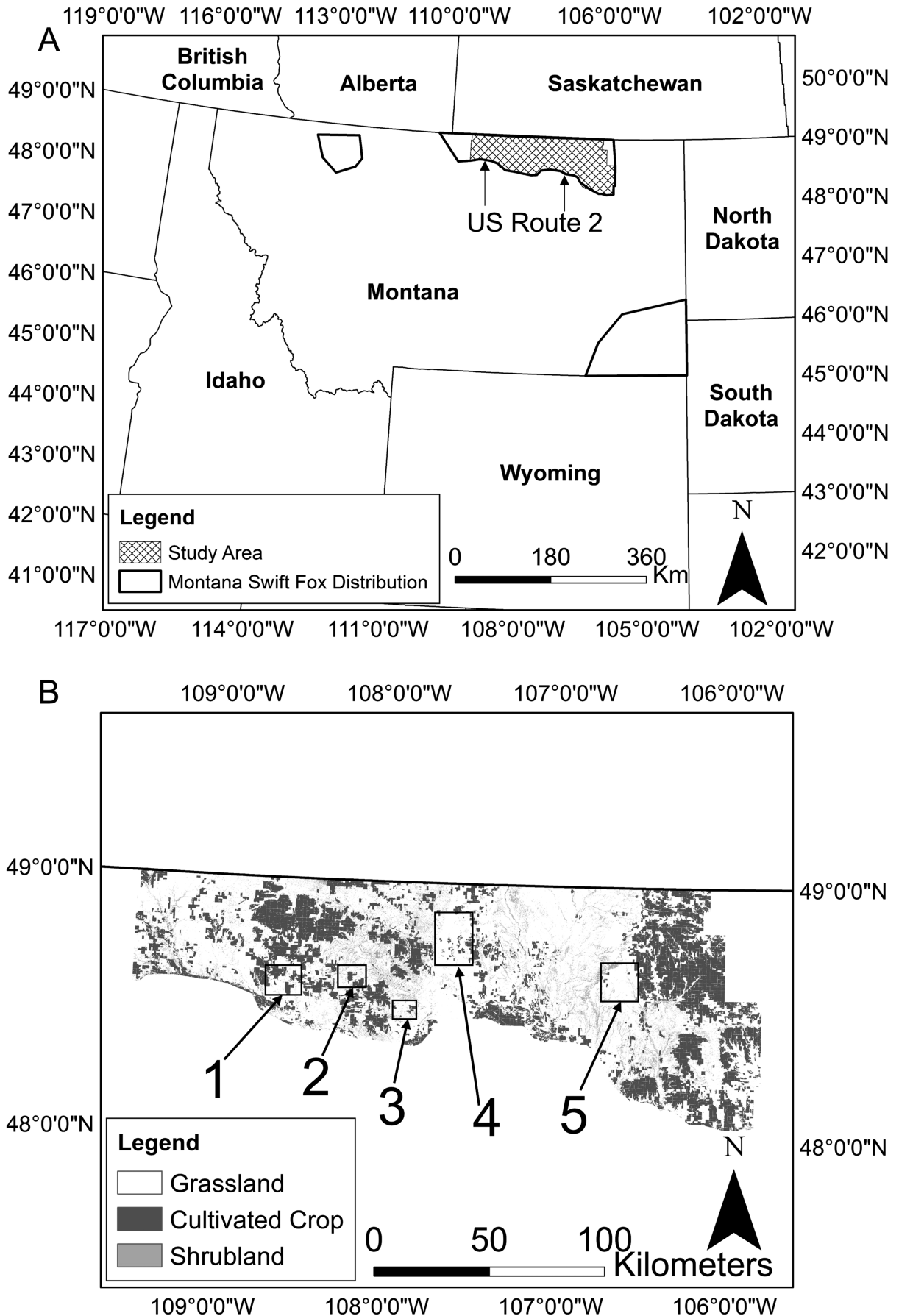
Fig. 1.—(A) Swift fox, *Vulpes velox*, distribution and study area in Montana where we estimated home range size and resource use during 2016–2018, and (B) Areas within the study area where we trapped six (1), four (2), three (3), twenty-two (4), and thirteen swift foxes (5) in 2016–2018.

we removed locations with less than three satellites and a DOP value greater than 10.

Home range size.—We monitored swift foxes for an average of 110 days (range: 31–225 days) and estimated the home range size of each swift fox for which we collected at least 30 locations (Seaman et al. 1999), which we considered to be representative of each individual's annual home range. For each swift fox, we generated a 99% utilization distribution (UD) with package *ks* in program R (R Core Team 2018) using the fixed kernel density estimator (Worton 1989; Seaman and Powell 1996) with plug-in bandwidth (Gitzen et al. 2006). We estimated the home range size of each swift fox by calculating the area within the 99% volume contour, to be comparable with home range estimates from a nearby study by Moehrenschlager et al. (2007). We used the Shapiro–Wilk test to test the hypothesis that home range sizes were normally distributed. Home range sizes were skewed to the left and therefore we rejected the normality hypothesis ($W = 0.88$, $P = 0.009$). We therefore log-transformed the home range sizes. Because these were normally distributed after log-transformation ($W = 0.98$, $P = 0.95$), we used these in further analyses. We conducted three-way analysis of variance (ANOVA) to determine if there was a difference in the average 99% home range size due to field season, age class, or sex. Significant effects were further investigated with Tukey's honestly significant difference (HSD) procedure. We also estimated the home range size of each swift fox by calculating area within the 95% volume contour to be comparable with other studies (Table 1) and conducted the same ANOVA test for the 95% fixed kernel home ranges.

We also were interested in the relationship between the level of cropland within a home range and home range size. First, we calculated the percentage of cropland, as defined by the National Land Cover Database (NLCD—Xian et al. 2015), within the 99% home range of each individual. We then log-transformed home range size and the percentage of cropland within the home range to meet assumptions of normality. Lastly, we used simple linear regression and Pearson's correlation to assess the relationship between home range size and percentage of cropland.

Creating resource layers.—We identified from the literature nine variables (Table 2) that we predicted would influence how swift foxes used the landscape. We predicted that loam soils would have a positive influence on space use because they are soft soils in which to dig dens, and that other soil types would have a negative influence (Hines 1980; Olson 2000), with clay loam serving as the reference category for soil types in the resource use analysis because it was the most widespread soil type. We created a map of soil types using data from the U.S. Department of Agriculture (USDA) Natural Resources Conservation Service, Soil Survey Geographic soils database (https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx). We classified soil data into six types (clay, clay loam, loam, sand, silt, and other [a combination of plant material, peat, and bedrock]) based on the USDA soil texture classification (Soil Science Division Staff 2017) following the methods outlined in Lahatte and Pradhan (2016). We predicted that a greater proportion of shrub cover would negatively influence swift fox space use because they would avoid these areas due to high predation risk from coyotes, which select for these areas, and decreased detection of predators by swift foxes (Harrison and Schmitt 2003; Thompson and Gese 2007). We used data of shrub cover, quantified as the proportion of shrub canopy in a 30×30 m cell, using the NLCD. We predicted that a greater proportion of grassland would have a positive influence on space use because the proportion of grassland has been found to be important in a past study of swift fox occupancy (Martin et al. 2007). We calculated the proportion of grassland landcover type from the NLCD within a 1-km radius circular moving window in

Table 2.—Variables predicted to influence resource use by swift foxes, *Vulpes velox*, in northeastern Montana during 2016–2018 with their abbreviation, description, units, prediction, range, and supporting citation. Shrub = proportion of shrub canopy, TRI = topographic roughness index, NDVI = normalized difference vegetation index, PG = percent grassland, Paved = distance to paved road, UnPaved = distance to gravel road, DistCrop = distance to crop field, DistWell = distance to gas well. *B* = beta coefficient such that $B < 0$ indicates that the coefficient is less than zero indicating a negative relationship and $B > 0$ indicates a positive relationship. All variables were continuous except for soil type which was categorical.

Resource variable	Description	Prediction	Range	Citation
Soil type[a]	Soil types based on the USDA Texture Triangle[b]			Hines (1980)
Clay		$B < 0$		
Loam		$B > 0$		
Sand		$B < 0$		
Silt		$B < 0$		
Other	Combination of plant material, peat, bedrock	$B < 0$		
Shrub	Percent of shrub canopy in each 30×30m raster cell (%)	$B < 0$	0–72	Thompson and Gese (2007)
TRI	Surface roughness from level—rough	$B < 0$	0–40	Russell (2006)
NDVI	Normalized difference vegetation index	$B < 0$	0.2–0.74	Thompson and Gese (2007)
PG	Percent of cells as grassland in a 1 km circular moving window (%)	$B > 0$	0–100	Martin et al. (2007)
Paved	Distance to nearest paved road (m)	$B < 0$	0–6,825	Nevison (2017)
UnPaved	Distance to nearest gravel road (m)	$B < 0$	0–6,826	Hines and Case (1991)
DistCrop	Distance to nearest cultivated crop edge (m)	$B < 0$	0–5,544	Sovada et al. (2003)
DistWell	Distance to nearest active natural gas well (m)	$B < 0$	0–33,985	Moll et al. (2018)

[a]Clay loam was the reference category.

[b]Science Division Staff. 2017. Soil Survey Manual. Government Printing Office, Washington D.C.

ArcGIS 10.3.1 (ESRI, Redlands, California). We predicted that greater topographic roughness (see below) would have a negative influence on swift fox space use because rough topography can inhibit visual predator detection by swift foxes (Russell 2006). We estimated topographic roughness of the study area by calculating the Terrain Roughness Index (Riley et al. 1999) across a 30-m digital elevation model, which compared the differences between the altitude of a cell and the eight surrounding cells. Values close to zero indicate level terrain and larger values indicate more rugged terrain (Riley et al. 1999). We predicted that greater vegetation productivity would have a negative effect on swift fox space use because larger canids select these areas and outcompete swift foxes in them (Phillips et al. 2003; Nelson et al. 2007; Thompson and Gese 2007). Selection for high productivity areas by canids is likely in part due to a positive relationship between environmental productivity and small mammal abundance (Munkhzul et al. 2012; Smith et al. 2017). In addition, high productivity habitats in our study system typically occurred near rivers or adjacent areas where irrigated crop field were developed—two landscape features known to be selected for by red fox (*Vulpes vulpes*) and coyotes (Sargeant et al. 1987; Kamler et al. 2005). Assessment of environmental productivity thus is likely to provide a higher resolution index of potential interspecific competition between swift fox and other canids than categorical landcover covariates alone. To account for productivity in our analysis, we used data from normalized difference vegetation index (NDVI), which is a measure of the difference between near-infrared (strongly reflected by vegetation) and red light (absorbed by vegetation), such that high values (+1) indicate more vegetative growth and lower values (-1) indicate sparse vegetation or senescence. We obtained these data from NASA's Land Process Distributed Active Archive Center and calculated NDVI as the average of the maximum value between May and September during 2017 and 2018.

We also identified four anthropogenic features from our literature review that we predicted would influence swift fox resource use (Table 2). We predicted that greater distance to cultivated crop fields would have a negative effect because crops were harvested or fallow during our study and thus available to swift foxes (Sovada et al. 2003). We predicted that greater distance to paved and unpaved roads would negatively influence space use because swift foxes might use these areas as travel corridors and to avoid coyotes (Hines and Case 1991; Clevenger et al. 2010). Coyotes are known to be highly adaptable and use areas of high human activity, and even reside in urban areas (Riley et al. 2003; Gehrt et al. 2009; Grubbs and Krausman 2009; Murray and St Clair 2015). However, in our study area, human density was extremely low (less than one person per square mile) and coyotes were frequently removed lethally whenever they were seen due to perceived conflicts with livestock producers. We predicted that coyotes would, therefore, avoid areas of more intensive human activity, such as near active gas wells that are regularly visited for maintenance, and that as a result, these areas would be selected for by swift foxes (Cypher et al. 2000). We estimated risk of encountering humans by calculating distance to cultivated crop fields, paved roads, unpaved roads, and gas wells, in ArcGIS 10.3.1, as the Euclidean distance from the edge of

cultivated crop field (raster values inside a crop field had a value of zero) from the 2011 NLCD (Homer et al. 2015), distance from paved and unpaved roads (Montana State Library, downloaded April 2017, http://geoinfo.msl.mt.gov/data), and active gas well sites (Montana Department of Natural Resources and Conservation Board of Oil and Gas Conservation, downloaded September 2018, http://dnrc.mt.gov/divisions/board-of-oil-and-gas-conservation). All variables were spatially mapped across the study area as raster layers, except the soil type layer, which was mapped as a vector layer.

Resource use.—We used resource utilization functions (RUFs—Marzluff et al. 2004) to evaluate resource use of each swift fox within the home range (third-order scale sensu Johnson 1980). Resource utilization functions treat resource use as a continuous process rather than a binary process (i.e., used or not used), and use a multiple regression framework to compare differential space use to environmental features while accounting for spatial autocorrelation (Marzluff et al. 2004; Kertson and Marzluff 2011). For each swift fox, we created a grid of points for each UD and rescaled values to a scale of 0 (lowest use) to 100 (highest use). In order to log-transform the UD values for analysis, we added 0.01 to all UD values, then log-transformed the UD values to meet assumptions of normality (Hooten et al. 2013). At each grid point, we extracted the values of the nine underlying covariate layers for each swift fox. We used the log-transformed UD values as the response variable in the multiple regression analysis (Marzluff et al. 2004). Prior to analysis, we screened all covariates for multicollinearity using Pearson's correlation ($r > 0.7$) and scaled them to mean = 0 and centered them to variance = 1. When there was a correlation greater than 0.7, we removed one of the variables from analysis. We used the *ruf* package (Handcock 2012) in program R to perform the analysis.

Based on previous studies of swift fox resource use, we developed 16 a priori models of how swift foxes use resources in the landscape (Table 3). We evaluated support for each model using Akaike's Information Criterion adjusted for small sample size (AIC$_c$—Burnham and Anderson 2002) to identify

Table 3.—A priori models developed from competing hypotheses for swift fox, *Vulpes velox*, resource use in northeastern Montana during 2016–2018.

Hypothesis	Model
No factors	Null
Predation risk and den availability	TRI
	NDVI
	PG
	TRI + NDVI
	TRI + PG
	Shrub + TRI + NDVI
	Soil Type + Shrub + TRI + NDVI + PG
Anthropogenic features	Paved + UnPaved
	DistCrop
	Paved + UnPaved + DistCrop
	DistWell + DistCrop
	Paved + UnPaved + DistCrop + DistWell
Sub global	TRI + PG + Paved + UnPaved + DistCrop
	Soil Type+ Shrub + NDVI + DistWell
Global	Soil Type + Shrub + TRI + NDVI + PG + Paved + UnPaved + DistCrop + DistWell

the top-ranked model based on Akaike weights (w_i), with a top model having the majority of the model weight. Based on the top-ranked model, we used standardized beta-coefficients to assess inter-individual variability in resource use patterns. In addition, we developed a population-level RUF by averaging beta-coefficients from top models across all individuals and calculating the associated variance (Marzluff et al. 2004). We considered variables with 95% confidence intervals around beta estimates that did not overlap zero to influence resource use.

We evaluated the predictive performance of the population-level model using k-fold cross-validation (Boyce et al. 2002). For cross-validation, we randomly designated 20% of the UD cells of an individual swift fox as the testing set and estimated the RUF coefficients again using the remaining 80% of UD cells (training set). We repeated this process 10 times to create 10 sets of testing and training data. We then used the RUF coefficients from the training data to estimate the UD values of the testing data set. We calculated the Pearson's correlation coefficient among all iterations of the actual UD values of the testing set with the predicted UD values of the training sets. We then averaged the individual correlation coefficients across all swift foxes to create a population level correlation coefficient. We expected the models with a strong predictive ability to have a high correlation coefficient.

RESULTS

Capture and monitoring.—We captured 46 swift foxes during 2016 and 2017 at five areas (Fig. 1B). We obtained at least 30 locations from 22 individuals (13 males and 9 females) during October through March 2016–2017 and October 2017–May 2018 for use in our analysis. One male was captured in both 2016 as a juvenile and 2017 as an adult. We treated data from each year independently because 183 days elapsed between the last location from 2016 to 2017 and the first location of 2017–2018; in addition, environmental conditions and areas of use varied between years. On average, we collected 267 locations (SE = 41, range = 35–550) per swift fox; there was no statistical difference between number of locations collected per swift fox between 2016 and 2017 and 2017 and 2018 (t_{21} = 1.48, P = 0.16) despite the fact that swift foxes in 2017–2018 were monitored for a statistically significant greater number of days (t_{21} = -2.10, P = 0.048). The average GPS location success was 50% (SE = 2.4%, range = 26–80%); we attribute most of the GPS location failure to swift foxes being in dens when collars were attempting locations as test collars had >93% location success.

Home range size.—We observed a significant effect of year ($F_{1,19}$ = 4.51, P = 0.047) on 99% fixed kernel home range size, but found no significant effect of sex ($F_{1,19}$ = 1.45, P = 0.24) or age ($F_{1,19}$ = 0.36, P = 0.56). We found that while 99% fixed kernel home range sizes were slightly larger in 2017–2018 (48.6 km^2 ± 6.9 km^2 [mean ± SE]) than 2016–2017 (33.5 km^2 ± 5.2 km^2), they were not significantly so when examined in light of Tukey's HSD procedure (P = 0.06). We, therefore, pooled sexes, age classes, and years, together to generate an average

99% fixed kernel home range size of 42.0 km^2 (SE = 4.7). We observed no significant effect of sex ($F_{1,19}$ = 1.35, P = 0.26) or age ($F_{1,19}$ = 0.32, P = 0.58) on the 95% fixed kernel home range sizes, but found a significant effect of year ($F_{1,19}$ = 4.91, P = 0.039). We found that 95% fixed kernel home range sizes were slightly larger in 2017–2018 (34.0 km^2 ± 4.5 km^2) than 2016–2017 (23.4 km^2 ± 3.5 km^2), but were not significantly so when using Tukey's HSD procedure (P = 0.053). We, therefore, pooled sexes, age classes, and years together to generate an average 95% fixed kernel home range size of 29.4 km^2 ± 3.1 km^2. Home range size was positively correlated to the amount of cropland within the home range (r = 0.39, n = 23; Fig. 2).

Resource use.—The global model received the most support (average w_i = 0.985) across all swift foxes; our population-level model, therefore, contained all covariates. Of the nine variables included in the population-level RUF, four were important to resource use (i.e., 95% CI did not overlap 0): topographic roughness index, proportion of grassland, distance from unpaved road, and distance to gas well (Table 4). These four variables also were more consistent in the direction of their effect across a larger percentage of individuals (>70% of swift foxes) compared to other variables (~50%; Table 4). We found that proportion of grassland had the largest influence on resource use (β_{PG} = 0.154), where the relative probability of use of an area by swift fox increased by 3.3% for every 1% increase in grasslands (Fig. 3a). The relative probability of use decreased by 7.9% and 7.4% for every kilometer away from unpaved roads (Fig. 3b) and gas well sites (Fig. 3c), respectively. The relative probability of use decreased by 3.0% and 11.3% for every unit increase in topographic roughness (Fig. 3d) and every 0.05 unit increase in NDVI, respectively (Fig. 3e). The model cross-validation results suggest that our population-level global model had weak predictive ability (r = 0.33).

DISCUSSION

We found the average home range size of swift foxes in northeastern Montana to be one of the largest recorded across their
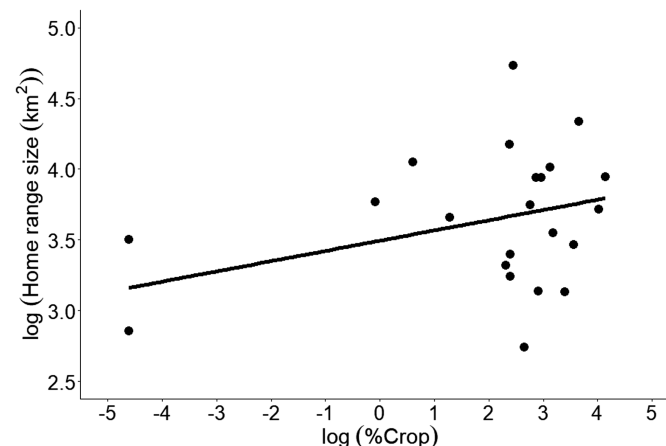

Fig. 2.—Relationship between 95% fixed kernel home range size and the percentage of home range composed of cropland for swift foxes, *Vulpes velox*, in northeastern Montana during 2016–2018.

Table 4.—Population-level resource use coefficients, variance, and 95% confidence intervals for the top model of swift foxes, *Vulpes velox*, in northeastern Montana during 2016–2018. We counted the number of swift foxes with positive or negative values for each coefficient.

| Variable	β	SE	Lower CI	Upper CI	Number of foxes	
					+	−
Intercept	1.062	0.339	0.723	1.401	20	3
Clay	−0.022	0.044	−0.066	0.022	9	14
Loam	−0.053	0.061	−0.114	0.008	5	16
Sand	−0.030	0.038	−0.067	0.008	7	14
Silt	−0.046	0.064	−0.110	0.018	9	14
Other	−0.033	0.036	−0.069	0.003	10	13
Shrub	−0.018	0.050	−0.068	0.031	11	12
TRI	−0.055	0.037	−0.092	−0.019	7	16
NDVI	−0.053	0.058	−0.110	0.005	4	19
PG	0.154	0.075	0.079	0.229	20	3
Paved	−0.023	0.187	−0.209	0.164	7	7
UnPaved	−0.104	0.092	−0.196	−0.011	9	12
DistCrop	−0.045	0.248	−0.293	0.203	13	10
DistWell	−0.108	0.082	−0.190	−0.026	5	17
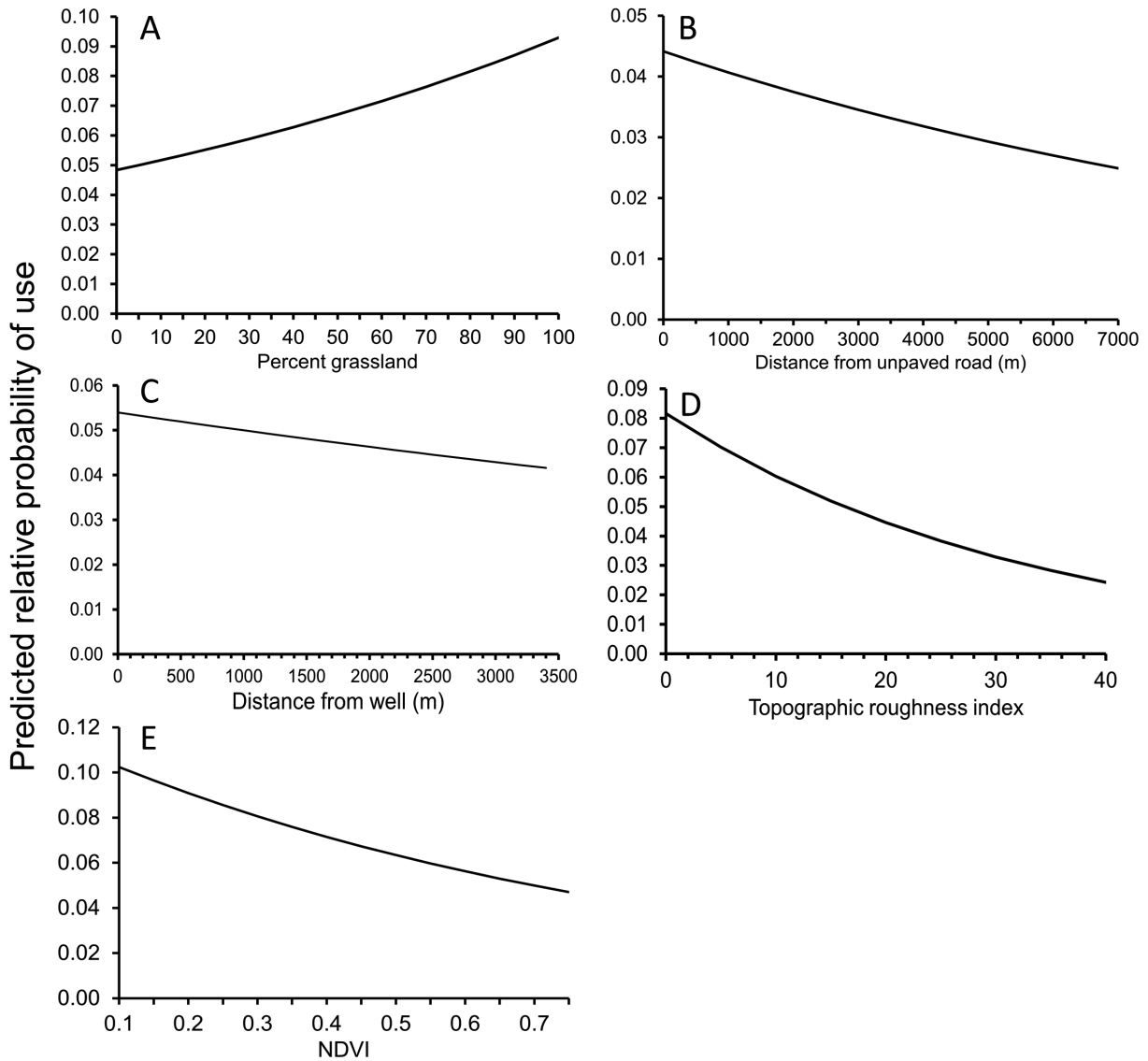
Fig. 3.—Relative probability-of-use curves for significant resource variables in resource utilization functions including (A) percent grassland, (B) distance from natural gas well, (C) distance from unpaved road, (D) topographic roughness, and (E) normalized difference vegetation index (NDVI) for swift foxes, *Vulpes velox*, in northeastern Montana, 2016–2018.

entire range. Our results are consistent with our prediction that swift fox home ranges are larger in the northern portion of the swift fox range than in the southern portion (Table 1). One possible explanation for why home range size is larger in the Northern Great Plains is that prey abundance is lower than in the southern portion of their range. Food abundance is believed to be the primary driver of intraspecific variation in animal home range size (reviewed by Mcloughlin and Ferguson 2000); this was the hypothesis proposed by Moehrenschlager et al. (2007) for why swift fox home ranges were larger in Canada. The hypothesis also was supported by White and Garrott (1997), who in reviewing the literature, found an inverse relationship of home range size of both swift fox and kit fox (*Vulpes macrotis*) with lagomorph density. However, given that the majority of our data came from the dispersal and breeding seasons (December–April), when swift fox home ranges have been observed to be largest (Hines 1980; Kitchen et al. 1999; Lebsock et al. 2012), it is possible that our results are biased toward a high estimate of annual home range size. Our estimates of swift fox home range size also are the first to be conducted with GPS collars. This might have provided a more accurate estimate of home range size that previous studies using VHF collars because we were able to obtain many locations that were not temporally or spatially biased due to surveyor effort (e.g., areas close to roads). Regardless, such large spatial requirements for swift foxes in this region have important implications for species recovery because managers need to ensure that large tracts of preferred habitat are available to swift foxes.

Our results indicate that proportion of grassland is the most important factor driving swift fox resource use. This has important implications because the Northern Great Plains are becoming increasingly fragmented by the conversion of prairie to cultivated crop fields (Comer et al. 2018). Swift foxes used areas primarily made up of grasslands, which in our study area were mostly used for cattle ranching, rather than areas dominated by row crop agriculture. We found a positive relationship between the amount of cropland and home range size in our study, which suggests that cultivated crop fields may have a negative impact on swift foxes by causing them to travel farther to obtain necessary resources such as food and denning sites (Mcloughlin and Ferguson 2000). Conservation programs that can preserve remaining large tracts of native grassland from the continued conversion to crop fields would benefit not only swift foxes, but other grassland specialist species as well. The Conservation Reserve Program (CRP) in particular has been essential for conservation of native grasslands, providing habitat for grassland birds and other native prairie species in areas dominated by cultivated crops (Niemuth et al. 2007). There is growing concern among managers and environmental organizations over the large amount of CRP contracts that will be ending because of the possibility that farmers and ranchers might convert their CRP fields to row-crop agriculture (Morefield et al. 2016; Hendricks and Er 2018) with negative impacts on grassland birds (Niemuth et al. 2007). Similarly, our findings suggest that swift foxes might be negatively impacted by extensive conversion of CRP fields to row-crop agriculture. However, at a fine spatiotemporal scale, swift foxes

in this region might at least temporarily use harvested row crop fields (Butler et al. 2019). Thus, the impact of conversion of native prairie to row-crop agriculture might not only be felt at a local scale, but at the landscape scale, given the large average home range size of swift foxes in this area.

Further, our results support our prediction that swift foxes might not actively avoid natural gas development. This is in contrast to the effects of natural gas development on other species in the region, such as greater sage-grouse (*Centrocercus urophasianus*—Holloran et al. 2015; Green et al. 2017); elk (*Cervus elaphus*—Buchanan et al. 2014); mule deer (Sawyer et al. 2006); and pronghorn (*Antilocapra americana*—Beckmann et al. 2012). While we did not collect data on the distribution of coyotes in the study area, we hypothesize that human activity around gas wells could have acted as a "human shield" (Berger 2007; Kuijper et al. 2015; Moll et al. 2018), where coyotes avoid these areas, thereby creating areas of low predation risk for swift foxes. A potentially confounding, but not mutually exclusive, hypothesis is that swift foxes used areas closer to wells because wells were built on areas of flat topography, and swift foxes might, therefore, be selecting for topography rather than the gas wells themselves. However, we did not find a high correlation between topographic roughness and distance to well, and if topographic roughness was the main driver, we would expect to find no relationship between distance to gas well and space use. Finally, it could be that gas wells in our study area were not present at a high enough density to have a negative impact on swift fox space use. These findings are consistent with studies on San Joaquin kit foxes that found these animals occupied areas of low to medium oilfield development, but were absent from areas of high-development, potentially due to the abundance of coyotes in high development areas (Fiehler et al. 2017). It could be that oil development in our study area had not reached the threshold level where it would begin to have a negative impact on swift foxes.

Consistent with previous swift fox studies and our predictions, we found that swift foxes used areas closer to unpaved roads, which suggests that unpaved roads do not act as barriers for movement. Swift foxes might use areas on and adjacent to roads for three reasons: (1) the availability of roadkill and small mammals (Hines and Case 1991; Klausz 1997); (2) use as a travel corridor (Hines and Case 1991; Pruss 1999; Nevison 2017); and (3) avoidance of coyotes (Kamler et al. 2003a; Nevison 2017). While we did not quantify carrion amounts on roads, we frequently observed road-killed birds, snakes, leporids, and Richardson's ground squirrels (*Urocitellus richardsonii*) that would be available for swift foxes to scavenge. We occasionally observed swift foxes on roads while conducting radio telemetry monitoring, potentially seeking out carrion or using the elevated roads to enhance visual detection of predators. We did not quantify coyote space use in this study, although similar to gas well development, roads could act as a "human shield" on account of which coyotes avoid these areas (Roy and Dorrance 1985; Sargeant et al. 1987; Kamler et al. 2003b) due to the potential of being killed by humans. Similarly, Cypher et al. (2009), noted that in central California, people attempted to hunt coyotes from the road, which might have caused coyotes

to avoid roads. However, there also are several studies from other parts of the coyote's range that demonstrate their frequent use of roads (Grinder and Krausman 2001; Hinton et al. 2015; Murray and St Clair 2015). It is possible that swift fox avoidance of coyotes on roads has a temporal component with avoidance occurring on a scale of hours, rather than on a longer scale. In contrast, swift foxes collared in our study did not select for areas adjacent to or overlapping paved roads, which supports our original prediction that US Route 2 could be acting as a barrier to swift fox movement and dispersal. However, this could have been an artifact of the low paved road density in our study area and our failure to collar foxes adjacent to paved roads. Research from Badlands National Park indicated that swift foxes selected dens closer to roads and were observed traveling on paved roads and crossing an interstate highway (Clevenger et al. 2010; Nevison 2017). San Joaquin kit foxes also have been found to cross paved roads (Cypher et al. 2009).

In contrast to our hypothesis that swift foxes would use resources that minimize predation risk, topographic roughness only had a marginal influence on swift fox resource use in this study. Swift foxes generally are thought to prefer to use areas of level to rolling topography and avoid steep areas (Loy 1981; Olson 2000; Russell 2006), likely in an attempt to enhance detecting potential predators (Cameron 1984). While we found marginal support for a negative effect of increasing topographic roughness similar to previous swift fox studies, and those on San Joaquin kit foxes (Warrick and Cypher 1998), the effect of topographic roughness was small (β_{TRI} = -0.055). We offer two, non-mutually exclusive explanations for why the effect of topographic roughness was small. First, to enhance our ability to catch a sufficient number of individuals, we trapped in areas that we expected to be good swift fox habitat that were not near steep coulees or badland areas. Second, it is possible that because we only investigated resource use within the home range (i.e., third-order selection), swift foxes might have selected the location of their home ranges away from the roughest topography of the area (i.e., second-order selection).

In accordance with our predictions, swift fox space use was negatively influenced by areas with higher primary productivity where inter-specific competition and predation pressure likely were highest. Although the 95% confidence intervals of NDVI overlapped zero (-0.110, 0.005), we believe it to be ecologically influential. In our study area, high NDVI values primarily were associated with plains cottonwood (*Populus deltoides*) forests and irrigated crop fields. Past studies have found that swift foxes avoid forests as well as crop fields, possibly because these areas inhibit predator detection (Kamler et al. 2003a; Sasmal et al. 2011). Swift foxes also might avoid crop fields because of competition with red foxes. Nonnative red foxes occur in the region through eastward range expansion, having arrived during the 1960s (Kamler and Ballard 2002). Red foxes, of European origin, are thought to be better adapted to human-impacted environments such as agricultural areas (Kamler and Ballard 2002). In a concurrent camera trapping study, red foxes in our study area were most frequently detected near areas with a high proportion of cultivated crop

fields (A. Butler, Clemson University, pers. obs.). This is consistent with previous research that has found that coyotes exclude red foxes from open areas through competition and direct mortality, causing red foxes to restrict their movements to near anthropogenic development (Cypher et al. 2001). Moreover, prior research found that resident coyotes selected farmlands in the summer, but native prairie in the winter (Kamler et al. 2005).

Our research sheds light on the spatial and resource requirements of swift foxes, and provides important information for long-term management strategies to improve population connectivity of this species. Swift fox conservation in the Northern Great Plains might be particularly challenging because of the large spatial requirements of swift foxes in this region, likely requiring wildlife managers to work across individual property boundaries. We therefore encourage wildlife managers and conservation groups to work with local ranchers to maintain their pastures as native prairie with the goal of maintaining large tracts of intact grassland that are likely to support natural range expansion. Swift foxes can be added to a list of species in the Northern Great Plains, along with pronghorn (Jakes et al. 2018) and sage grouse (Tack et al. 2012), for which conservation success likely will require the creation and maintenance of large north-south corridors of native grassland that allow these species to migrate and disperse.

Literature Cited

ALEXANDER, J. L., S. K. OLIMB, K. L. S. BLY, AND M. RESTANI. 2016. Use of least-cost path analysis to identify potential movement corridors of swift foxes in Montana. Journal of Mammalogy 97:891–898.

AUSBAND, D. E., AND K. R. FORESMAN. 2007. Dispersal, survival, and reproduction of wild-born, yearling swift foxes in a reintroduced population. Canadian Journal of Zoology 85:185–189.

BECKMANN, J. P., K. MURRAY, R. G. SEIDLER, AND J. BERGER. 2012. Human-mediated shifts in animal habitat use: sequential changes in pronghorn use of a natural gas field in Greater Yellowstone. Biological Conservation 147:222–233.

BERGER, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

BOYCE, M. S., P. R. VERNIER, S. E. NIELSEN, AND F. K. A. SCHMIEGELOW. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Buchanan, C. B., J. L. Beck, T. E. Bills, and S. N. Miller. 2014. Seasonal resource selection and distributional response by elk to development of a natural gas field. Rangeland Ecology and Management 67:369–379.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2nd ed. Springer. New York.

Butler, A. R. et al. 2019. Winter movement behavior by swift foxes (*Vulpes velox*) at the northern edge of their range. Canadian Journal of Zoology 97:922–930.

Cameron, M. W. 1984. The swift fox on the Pawnee National Grassland: its food habits, population dynamics and ecology. M.A. thesis, University of Northern Colorado. Greeley, Colorado.

Carbyn, L. N. 1998. Update COSEWIC assessment and update status report on the swift fox in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Canada.

Clevenger, A. P., A. V. Kociolek, and B. L. Cypher. 2010. Effects of four-lane highways on desert kit fox and swift fox: inferences for the San Joaquin kit fox population. Western Transportation Institute, Montana State University. Bozeman, Montana.

Comer, P. J., J. C. Hak, K. Kindscher, E. Muldavin, and J. Singhurst. 2018. Continent-scale landscape conservation design for temperate grasslands of the Great Plains and Chihuahuan Desert. Natural Areas Journal 38:196–211.

Cypher, B. L. et al. 2000. Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. Wildlife Monographs 145:1–43.

Cypher, B. L., C. D. Bjurlin, and J. L. Nelson. 2009. Effects of roads on endangered San Joaquin kit foxes. Journal of Wildlife Management 73:885–893.

Cypher, B. L., H. O. Clark, P. A. Kelly, C. V. H. Job, G. D. Warrick, and D. F. Williams. 2001. Interspecific interactions among wild canids: implications for the conservation of endangered San Joaquin kit foxes. Endangered Species Update 18:171–174.

Dowd Stukel, E. 2011. Conservation assessment and conservation strategy for swift fox in the United States – 2011 update. South Dakota Department of Game, Fish and Parks. Pierre, South Dakota.

Fiehler, C. M., B. L. Cypher, and L. R. Saslaw. 2017. Effects of oil and gas development on vertebrate community composition in the southern San Joaquin Valley, California. Global Ecology and Conservation 9:131–141.

Gehrt, S. D., C. Anchor, and L. A. White. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? Journal of Mammalogy 90:1045–1057.

Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. Journal of Wildlife Management 70:1334–1344.

Green, A. W., C. L. Aldridge, and M. S. O'donnell. 2017. Investigating impacts of oil and gas development on greater sage-grouse. Journal of Wildlife Management 81:46–57.

Grinder, M. I., and P. R. Krausman. 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. Journal of Wildlife Management 65:887–898.

Grubbs, S. E., and P. R. Krausman. 2009. Use of urban landscape by coyotes. The Southwestern Naturalist 54:1–12.

Güthlin, D., et al. 2011. Estimating habitat suitability and potential population size for brown bears in the Eastern Alps. Biological Conservation 144:1733–1741.

Handcock, M. S. 2012. Estimates of the resource utilization function. Version 1.5–2. University of California-Los Angeles. Los Angeles, California. http://www.csde.washington.edu/~handcock/ruf/. Accessed 26 November 2017.

Harrison, R. L., and C. G. Schmitt. 2003. Current swift fox distribution and habitat selection within areas of historical occurrence in New Mexico. Pp. 71–77 in The swift fox: ecology and conservation of swift foxes in a changing world (M. A. Sovada and L. N. Carbyn, eds.). Canadian Plains Research Center, University of Regina. Regina, Saskatchewan.

Hendricks, N. P., and E. Er. 2018. Changes in cropland area in the United States and the role of CRP. Food Policy 75:15–23.

Hines, T. D. 1980. An ecological study of *Vulpes velox* in Nebraska. M.S. thesis, University of Nebraska. Lincoln, Nebraska.

Hines, T. D., and R. M. Case. 1991. Diet, home range, movement, and activity periods of swift fox in Nebraska. Prairie Naturalist 23:131–138.

Hinton, J. W., F. T. van Manen, and M. J. Chamberlain. 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). PLoS ONE 10:e0132203.

Holloran, M. J., B. C. Fedy, and J. Dahlke. 2015. Winter habitat use of greater sage-grouse relative to activity levels at natural gas well pads. Journal of Wildlife Management 79:630–640.

Homer, C. G., et al. 2015. Completion of the 2011 national land cover database for the conterminous United States- representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Hooten, M. B., E. M. Hanks, D. S. Johnson, and M. W. Alldredge. 2013. Reconciling resource utilization and resource selection functions. The Journal of Animal Ecology 82:1146–1154.

Jakes, A. F., et al. 2018. Classifying the migration behaviors of pronghorn on their northern range. Journal of Wildlife Management 82:1229–1242.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kamler, J. F., and W. B. Ballard. 2002. A review of native and nonnative red foxes in North America. Wildlife Society Bulletin 30:370–379.

Kamler, J. F., W. B. Ballard, E. B. Fish, P. R. Lemons, K. Mote, and C. C. Perchellet. 2003a. Habitat use, home ranges, and survival of swift foxes in a fragmented landscape: conservation implications. Journal of Mammalogy 84:989–995.

Kamler, J. F., W. B. Ballard, R. L. Gilliland, and K. Mote. 2003b. Spatial relationships between swift foxes and coyotes in northwestern Texas. Canadian Journal of Zoology 81:168–172.

Kamler, J. F., W. B. Ballard, P. R. Lemons, R. L. Gilliland, and K. Mote. 2005. Home range and habitat use of coyotes in an area of native prairie, farmland and CRP fields. American Midland Naturalist 153:396–404.

Kertson, B. N., and J. M. Marzluff. 2011. Improving studies of resource selection by understanding resource use. Environmental Conservation 38:18–27.

Kitchen, A. M., E. M. Gese, and E. R. Schauster. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. Canadian Journal of Zoology 77:1645–1656.

Klausz, E. E. 1997. Small mammal winter abundance and distribution in the Canadian mixed grass prairies and implications for the swift fox. M.S. thesis, University of Alberta. Edmonton, Alberta.

Kuijper, D. P. J., J. W. Bubnicki, M. Churski, B. Mols, and P. Van Hooft. 2015. Context dependence of risk effects: wolves and tree logs create patches of fear in an old-growth forest. Behavioral Ecology 26:1558–1568.

LAHATTE, W. C., AND N. R. PRADHAN. 2016. Analysis of SURRGO data and obtaining soil texture classifications for simulating hydrologic processes. U.S. Army Engineer Research and Development Center. Vicksburg, Mississippi.

LEBSOCK, A. A., C. L. BURDETT, S. K. DARDEN, T. DABELSTEEN, M. F. ANTOLIN, AND K. R. CROOKS. 2012. Space use and territoriality in swift foxes (*Vulpes velox*) in northeastern Colorado. Canadian Journal of Zoology 90:337–344.

LOY, R. R. 1981. An ecological investigation of the swift fox (*Vulpes velox*) on the Pawnee National Grasslands, Colorado. M.S. thesis, University of Northern Colorado-Greeley. Greeley, Colorado.

MAGG, N., ET AL. 2016. Habitat availability is not limiting the distribution of the Bohemian-Bavarian lynx *Lynx lynx* population. Oryx 50:742–752.

MARTIN, D. J., G. C. WHITE, AND F. M. PUSATERI. 2007. Occupancy rates by swift foxes (*Vulpes velox*) in eastern Colorado. The Southwestern Naturalist 52:541–551.

MARZLUFF, J. M., J. J. MILLSPAUGH, P. HURVITZ, AND M. S. HANDCOCK. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85:1411–1427.

MCLOUGHLIN, P. D., AND S. H. FERGUSON. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience 7:123–130.

MITCHELL, E. L. 2018. Distribution, ecology, disease risk, and genetic diversity of swift fox (*Vulpes velox*) in the Dakotas. M.S. thesis, South Dakota State University. Brookings, South Dakota.

MOEHRENSCHLAGER, A., R. LIST, AND D. W. MACDONALD. 2007. Escaping intraguild predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift foxes. Journal of Mammalogy 88:1029–1039.

MOEHRENSCHLAGER, A., D. W. MACDONALD, AND C. MOEHRENSCHLAGER. 2003. Reducing capture-related injuries and radio-collaring effects on swift foxes. Pp. 107–113 in The swift fox: ecology and conservation of swift foxes in a changing world (M. A. Sovada and L. N. Carbyn, eds.). Canadian Plains Research Center, University of Regina. Regina, Saskatchewan, Canada.

MOEHRENSCHLAGER, A., AND C. MOEHRENSCHLAGER. 2018. Population survey of reintroduced swift foxes (*Vulpes velox*) in Canada and northern Montana 2014/2015. Centre for Conservation Research, Calgary Zoological Society. Calgary, Alberta, Canada.

MOEN, R., J. PASTOR, Y. COHEN, AND C. C. SCHWARTZ. 2016. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60:659–668.

MOLL, R. J., ET AL. 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems 21:765–778.

MOREFIELD, P. E., S. D. LEDUC, C. M. CLARK, AND R. IOVANNA. 2016. Grasslands, wetlands, and agriculture: the fate of land expiring from the Conservation Reserve Program in the midwestern United States. Environmental Research Letters 11:1–9.

MTFWP. 2019. Montana swift fox conservation strategy. Montana Fish, Wildlife, and Parks. Helena, Montana.

MUNKHZUL, T., B. BUUVEIBAATAR, J. D. MURDOCH, R. P. READING, AND R. SAMIYA. 2012. Factors affecting home ranges of red foxes in Ikh Nart. Mongolian Journal of Biological Sciences 10:51–58.

MURRAY, M. H., AND C. C. ST CLAIR. 2015. Individual flexibility in nocturnal activity reduces risk of road mortality for an urban carnivore. Behavioral Ecology 26:1520–1527.

NELSON, J. L., B. L. CYPHER, C. D. BJURLIN, AND S. CREEL. 2007. Effects of habitat on competition between kit foxes and coyotes. Journal of Wildlife Management 71:1467–1475.

NEVISON, S. A. 2017. Swift foxes in southwestern South Dakota: assessing the current status of a reintroduced population. M.S. thesis, South Dakota State University. Brookings, South Dakota.

NIEMUTH, N. D., F. R. QUAMEN, D. E. NAUGLE, R. E. REYNOLDS, M. E. ESTEY, AND T. L. SHAFFER. 2007. Benefits of the conservation reserve program to grassland bird populations in the prairie pothole region of North Dakota and South Dakota. Final report to United States Department of Agriculture Farm Service Agency Reimbursable Fund Agreement OS-IA-04000000-N34.

OLSON, T. L. 2000. Population characteristics, habitat selection patterns, and diet of swift foxes in southeast Wyoming. M.S. thesis, University of Wyoming. Laramie, Wyoming.

PECHACEK, P., F. G. LINDZEY, AND S. H. ANDERSON. 2000. Home range size and spatial organization of Swift fox Vulpes velax (Say, 1823) in southeastern Wyoming. Mammalian Biology 65:209–215.

PHILLIPS, M. L., W. R. CLARK, M. A. SOVADA, D. J. HORN, R. R. KOFORD, AND R. J. GREENWOOD. 2003. Predator selection of prairie landscape features and its relation to duck nest success. Journal of Wildlife Management 67:104–114.

POWELL, R. A., AND M. S. MITCHELL. 2012. What is a home range? Journal of Mammalogy 93:948–958.

PRUSS, S. D. 1999. Selection of natal dens by the swift fox (*Vulpes velox*) on the Canadian prairies. Canadian Journal of Zoology 77:646–652.

RILEY, S. P. D., ET AL. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566–576.

RILEY, S., S. D. DEGLORIA, AND R. ELLIOT. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:23–27.

ROY, L. D., AND M. J. DORRANCE. 1985. Coyote movements, habitat use, and vulnerability in central Alberta. Journal of Wildlife Management 49:307–313.

RUSSELL, T. A. 2006. Habitat selection by swift foxes in Badlands National Park and the surrounding area in South Dakota. M.S. thesis, South Dakota State University. Brookings, South Dakota.

SARGEANT, A. B., S. H. ALLEN, AND J. O. HASTINGS. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. Journal of Wildlife Management 51:285–293.

SASMAL, I., ET AL. 2011. Habitat selection by female swift foxes (*Vulpes velox*) during the pup-rearing season. Prairie Naturalist 43:29–37.

SASMAL, I., ET AL. 2015. Release method evaluation for swift fox reintroduction at Bad River Ranches in South Dakota. Restoration Ecology 23:491–498.

SAWYER, H., R. M. NIELSON, F. LINDZEY, AND L. L. MCDONALD. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

SEAMAN, D. E., J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDEKE, AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. The Journal of Wildlife Management 63:739–747.

SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

SETON, E. T. 1909. Life-histories of northern animals: an account of the mammals of Manitoba, vol. 1. Charles Scribner's Sons. New York.

SIKES, R. S. AND ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

SMITH, S. H., K. STEENHOF, C. J. MCCLURE, AND J. A. HEATH. 2017. Earlier nesting by generalist predatory bird is associated with human responses to climate change. The Journal of Animal Ecology 86:98–107.

SOIL SCIENCE DIVISION STAFF. 2017. Soil Survey Manual. Government Printing Office. Washington D.C.

SOVADA, M. A., C. C. SLIVINSKI, R. O. WOODWARD, AND M. L. PHILLIPS. 2003. Home range, habitat use, litter size, and pup dispersal of swift foxes in two distinct landscapes of western Kansas. Pp. 149–160 in The swift fox: ecology and conservation of swift foxes in a changing world (M. A. Sovada and L. N. Carbyn, eds.). Canadian Plains Research Center, University of Regina. Regina, Saskatachewan, Canada.

SOVADA, M. A., R. O. WOODWARD, AND L. D. IGL. 2009. Historical range, current distribution, and conservation status of the swift fox, *Vulpes velox*, in North America. Canadian Field-Naturalist 123:346–367.

TACK, J. D., D. E. NAUGLE, J. C. CARLSON, AND P. J. FARGEY. 2012. Greater sage-grouse *Centrocercus urophasianus* migration links the USA and Canada: a biological basis for international prairie conservation. Oryx 46:64–68.

THOMPSON, C. M., AND E. M. GESE. 2007. Food webs and intraguild predation: community interactions of a native mesocarnivore. Ecology 88:334–346.

WARRICK, G. D., AND B. L. CYPHER. 1998. Factors affecting the spatial distribution of San Joaquin kit foxes. Journal of Wildlife Management 62:707–717.

WHITE, P. J., AND R. A. GARROTT. 1997. Factors regulating kit fox populations. Canadian Journal of Zoology 75:1982–1988.

WORTON, B. J. 1989. Kernel methods for estimating the utlization distribution in home-range studies. Ecology 70:164–168.

XIAN, G., C. HOMER, M. RIGGE, H. SHI, AND D. MEYER. 2015. Remote sensing of environment characterization of shrubland ecosystem components as continuous fields in the northwest United States. Remote Sensing of Environment 168: 286–300.

ZIMMERMAN, A. 1998. Reestablishment of swift fox in north central Montana. M.S. thesis, Montana State University. Bozeman, Montana.

ZOELLICK, B. W., C. E. HARRIS, B. T. KELLY, T. P. O'FARRELL, T. T. KATO, AND M. E. KOOPMAN. 2002. Movements and home ranges of San Joaquin kit foxes (*Vulpes macrotis mutica*) relative to oil-field development. Western North American Naturalist 62:151–159.